

---

# JOURNAL OF THE ARNOLD ARBORETUM

---

VOL. 60

APRIL 1979

NUMBER 2

---

## BOREAL AND WESTERN NORTH AMERICAN PLANTS IN THE LATE PLEISTOCENE OF VERMONT<sup>1</sup>

NORTON G. MILLER AND GARY G. THOMPSON

MOST QUATERNARY PALEOBOTANICAL STUDIES are aimed at determining floristic composition and vegetation types, and from these, by inference, climates and other environmental features of the past. In North America little use has been made of the Pleistocene and Holocene fossil plant record to explain development of distribution patterns of plants other than trees. No doubt this is because fully identified megascopic plant remains are known from relatively few localities when compared with Britain and northern parts of Europe, for which there are admirable syntheses of historical phytogeography based on fossils (e.g., Godwin, 1975).

We report here on a reinvestigation of fossiliferous lake sediments that contain many phytogeographically noteworthy species. The deposit is located in the upper Connecticut River valley near Colebrook, New Hampshire, and was discovered in the late 1920's by R. J. Lougee. Arthur Hollick (1931) treated plant fossils from the deposit in one of the first detailed reports of a North American late glacial leaf flora. Unfortunately, Hollick's specimens came from oxidized layers that contain only poorly preserved macrofossils. Our digging uncovered deeper, organic-rich lenses of unoxidized plant materials among which were wood fragments in sufficient quantity for radiocarbon dating. Pollen and spores were also found to be present throughout the section. This new material has permitted confirmation or revision of Hollick's determinations and an interpretation of the late glacial environment based on both pollen and plant macrofossils.

Megascopic Quaternary plant fossils have been reported from a few other places in New England. At sites near Hadley and Amherst, Massachusetts, in lake clays in the Connecticut River valley, Emerson (1898)

<sup>1</sup> We dedicate this paper to Stanley Jay Smith (20 September 1915–20 July 1978), Curator of Botany at the New York State Museum, ardent field botanist, and long-time student of the eastern North American flora and its geographic relationships.

© President and Fellows of Harvard College, 1979. No copyright is claimed for "A New *Herissantia* (Malvaceae) from the West Indies," which is the work of an employee of the U. S. Government.



noted leaves and fruits of several species of arctic-alpine flowering plants. More recently, Ashley (1972) reported fossil leaves (including a specimen identified as *Vaccinium ?uliginosum* L.) in clays of glacial Lake Hitchcock from several places in Massachusetts and Connecticut. Fossils of arctic and alpine plants, most notably *Salix herbacea* L. and *Dryas integrifolia* Vahl, have also been found in late glacial clays at Cambridge, Massachusetts (Argus & Davis, 1962). The flora reported by Hollick (1931) differed from these, however, in containing leaves of trees. Our new fossil assemblages show that trees (balsam poplar and spruce) indeed occurred near the site, but that surfaces were mostly covered by an open vegetation of herbs and low woody plants intolerant of shade.

Among the terrestrial plants listed by Hollick (1931), we confirm the presence of *Populus balsamifera* L., *Dryas Drummondii* Richardson, and possibly *Salix argyrocarpa* Andersson and/or *S. pellita* Andersson, but we found no specimens of *S. pedicellaris* Pursh or *Vaccinium angustifolium* Aiton. Previously unrecognized species are added to the flora, and revisions are suggested for Hollick's material of *Salix reticulata* L., *Celtis occidentalis* L., *Loiseleuria procumbens* (L.) Desv., *Kalmia polifolia* Wengenh., and *Vaccinium macrocarpon* Aiton. Some of the species represented by fossils now have an eastern-western North American disjunct distribution. The fossils establish that such present-day disjuncts once grew in eastern North America south of their present areas of occurrence. Furthermore, they grew at low elevations on surfaces that had been recently freed of glacial ice.

## GEOLOGIC SETTING

### REGIONAL DESCRIPTION AND GLACIAL HISTORY

The plant fossils occur in sediments exposed on the west bank of the Connecticut River in Lemington Township, Essex County, Vermont (FIGURE 1). The fossil locality, which we designate the Columbia Bridge Site, is at lat. 44°50'50" N., long. 70°38'30" W., 0.8 km. south of the Columbia Bridge (a wooden covered bridge). The site is at an elevation of 301 meters in the Northeastern Highlands of Vermont, a northwestern extension of the White Mountains of New Hampshire (Fenneman, 1938; Jacobs, 1950). Relief is high, with Monadnock Mountain (elev. 957 m.) just 4 km. north of the site. Metamorphic rocks (chlorite- to sillimanite-grade metasediments) underlie most of the area (Myers, 1964).

A thin, discontinuous mantle of till is spread over the uplands near the site. Thicknesses are generally less than 7 meters, in contrast to those in valleys, where till over 30 meters thick has been measured (Stewart & MacClintock, 1969). Stewart and MacClintock (1969) reported two types of till in the region. One is a "dense, compact till," with more erratic fragmental material than the second, which has a higher percentage of local bedrock fragments.

On the basis of till fabric, Stewart and MacClintock (1969) recognize



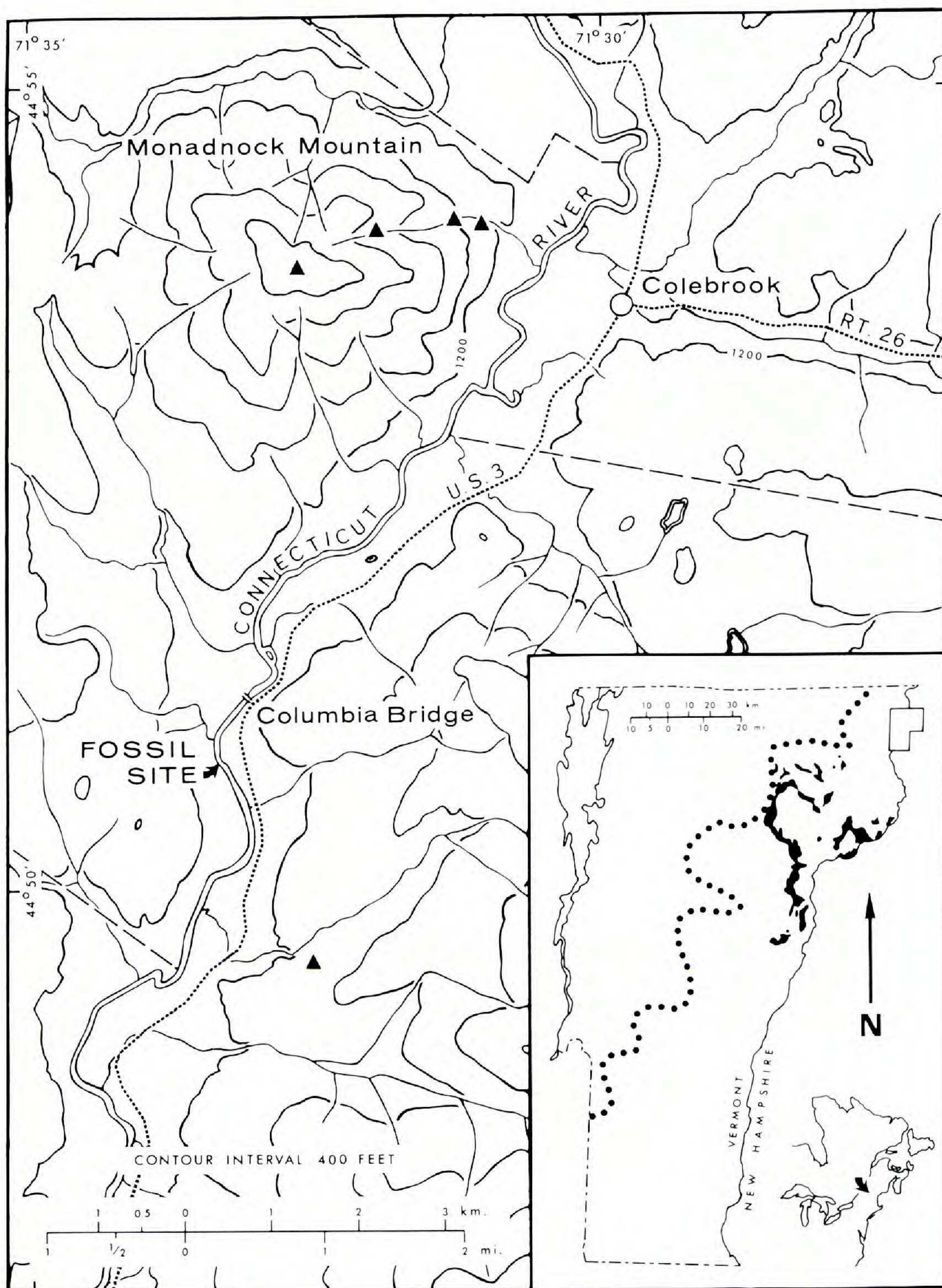


FIGURE 1. Topographic map of upper Connecticut River valley showing location of Columbia Bridge site and places where surface pollen samples were obtained (black triangles). Inset: map of Vermont, kame moraines of Shelburne drift in black, Burlington drift border dotted, area of large scale map outlined. (Topographic base from U.S.G.S. Averill, Vermont-New Hampshire, and Dixville, New Hampshire, 15 min. quadrangles; inset map after Stewart & MacClintock, 1969.)



two tills of Wisconsinan age in the region: the Bennington (older), with a northwest-southeast fabric; and the Shelburne (younger), with a northeast-southwest fabric. A third, still younger till, the Burlington, with a northwest-southeast fabric, is recognized to the west of the area. Stewart and MacClintock have concluded that till fabric, as measured by their technique, shows ice-flow direction. Other evidence from Vermont (Flint, 1971, p. 178; Larsen, 1975; Wagner *et al.*, 1972) indicates that ice did not flow as Stewart and MacClintock have postulated, therefore the reality of the Bennington, Shelburne, and Burlington tills is controversial. Stewart and MacClintock interpret the Connecticut Valley glaciolacustrine sediments as having been deposited with the northward retreat of the Shelburne ice margin. They interpret landforms in the vicinity of St. Johnsbury, Vermont (FIGURE 1), as possibly being recessional moraines formed by Shelburne ice.

In Quebec, south of the St. Lawrence River, a sequence of dated moraines 12,800 to 11,000 years old (Gadd *et al.*, 1972) marks the retreat of the margin of the last glacier north of the Columbia Bridge site. Carbon-14 ages for the Champlain Sea, which occupied the St. Lawrence River and Champlain valleys, range from about 12,500 to 10,000 years B.P. (Cronin, 1977). Events reflected in Quebec may correlate with retreat of the Burlington ice in Vermont, although there are no supporting carbon-14 dates from Vermont where the ice margin position is marked by poorly developed moraines only (FIGURE 1; Stewart & MacClintock, 1969).

The chronology and process by which the continental glacier retreated from New England is still debated. Active zone retreat is indicated by recessional moraines and deformed sediment produced as a result of ice readvance, but few such features are found in northern Vermont. Stagnation zone retreat accounts for ice-contact features and an absence of recessional moraines. Recent data from Connecticut indicate an active ice margin in the Connecticut Valley (Larsen, 1978). Stone and Koteff (1973) interpret evidence in the Merrimac Valley, New Hampshire, as indicating active zone retreat, which Caldwell *et al.* (1978) have indirectly dated at about 13,500 years B.P. About 140 km. north of the locality of Caldwell *et al.*, an age of over 13,000 years has been reported recently from a lake basin on the flank of Mount Washington in the White Mountains (Spear, 1978).

As ice disappeared from New England, by whatever mechanism, lakes were dammed in valleys by the remaining ice or by drift deposited from it. The Connecticut Valley, being a main water course, contained large proglacial lakes. Lake Hitchcock, the largest and best documented of these, extended from a till dam at Rocky Hill, Connecticut, to Lyme, New Hampshire (Schafer & Hartshorn, 1965). North of Lake Hitchcock, and presumably younger, although less well documented, were Lakes Upham, Coös, and Colebrook (Lougee, 1939). Radiocarbon-dated pollen profiles from Connecticut bogs suggest a glacial readvance in southern New England shortly before 13,000 years B.P. (Flint, 1956). The date of Lake Hitchcock drainage, inferred from two carbon-14 age determinations, is



about 10,700 years B.P. (Flint, 1956), implying that Lake Hitchcock lasted 2000 to 3000 years. Antevs (1922), who worked out a varve record in Lake Hitchcock sediment of over 4000 years, inferred a much longer existence for the lake (see also Verosub, 1975). Prior to those reported in this paper, no carbon-14 dates had been directly determined from any lake sediment in the Connecticut Valley, nor have there been any radio-carbon dates that relate to the presumed younger lakes. The Columbia Bridge site is within the area of Lake Colebrook.

At Columbia Bridge the Connecticut Valley is narrow (0.6 km. wide), with relatively steep bedrock walls. Upstream from the site, along the flank of Monadnock Mountain, the valley is choked with high relief drift, and the river channel is restricted. This drift may have dammed a lake in the valley. Along the valley throughout this area is a complex arrangement of sediments and landforms which have been interpreted as deltas, beaches, kame terraces, eskers, and recent alluvium (Cannon, 1964; Stewart & MacClintock, 1970). Because lithologies composing these landforms may be similar and because there is no age control, we feel that a more detailed study of the surficial geology is required before the history of the valley lakes and river in this segment of the valley can be known. Such an interpretation is beyond the scope of this study.

#### DESCRIPTION AND INTERPRETATION OF SEDIMENTS

Lake sediment and alluvium crop out at the fossil site over an area of about 25 square meters where at least 3.5 meters of rhythmically laminated fossiliferous silt, sand, and clay is overlain by 4 meters of sand and silt. The lateral extent of the sediments is known in detail only within several meters of the exposure as a result of hand augering.

Sediments in the upper 4 meters grade uniformly from a basal orange to reddish brown, pebbly, coarse sand (with widely separated cobbles at the bottom) to light brownish yellow silt at the top. This upper unit contains small- and medium-scale cross laminations, which indicate current directions paralleling the crests of swells and the troughs of swales on the floodplain at the site. Thickness, particle size distribution, and current directions indicate that this unit is a recent point bar deposit. This deposit unconformably overlies the laminated unit, with an irregular contact. There is no evidence of how much laminated sediment was eroded before the deposition of the overlying sand unit.

The rhythmically laminated unit consists of alternating coarse and fine laminae. Fine-grained laminae range in thickness from 0.05 to 3.36 cm. ( $\bar{X}$  0.77 cm., s.d. 0.65); coarse-grained laminae from 0.08 to 3.48 cm. ( $\bar{X}$  0.64 cm., s.d. 0.57). The average couplet thickness is 1.39 cm. Pipette analysis of one fine-grained lamina revealed a mean grain size of 6.6  $\phi$  and a clay content of about 25 percent. This is coarser than the fine laminae of rhythmites in Lake Hitchcock sediments (Ashley, 1972). Coarse-grained laminae consist of silt and sand, with some exhibiting ripple cross-laminations. The clay-rich laminae are medium gray; silt and sand laminae



are light brownish yellow, except in the oxidized upper 0.75 meter, where the fine ones are light brownish yellow and the coarse ones reddish brown. Pebbles and one boulder ( $30 \times 21 \times 12$  cm.) were found widely spaced in the sediment. These are interpreted as dropstones from floating ice laden with coarse sediment.

We are unable to conclude definitely that all the rhythmites are varves. As is common among varves, many of the contacts between silt or sand and clayey silt beneath are sharp. Graded fine-grained laminae are known among summer layers attributed to spasmodic turbidity currents (Ashley, 1972). Among the Columbia Bridge rhythmites there are no megascopically obvious graded laminae, and a detailed pipette analysis showed no grading. On the other hand, winter layers tend to be of uniform thickness and grading throughout a sequence (Ashley, 1972). At Columbia Bridge the thickness of the fine-grained laminae is variable, and many of them contain thinner, coarse-grained laminae, making it difficult to recognize a winter layer. Although it is not possible to match such rhythmites with a varve category recognized by Ashley (1972) for Lake Hitchcock sediments, particle size data and the variation in lamina thickness compare most closely with her type II varves.

While it was difficult to count the number of couplets accurately, our best estimate is 116 between 0 and 1.65 meters. Fortuitous as it may be, radiocarbon dating of the interval 0.84–1.58 meters, which contains 66 couplets, indicates that as few as 75 or as many as 375 years may separate the dated levels. Thus, it is possible that paired laminae represent annual accumulations of sediment.

The laminated sediments are deformed. In the upper meter the laminae dip  $15^\circ$  south  $84^\circ$  west, and the uppermost are truncated at the unconformity. A few normal faults were seen in the exposure, and the strike of one of these was approximately north–south, with a dip to the east of about  $45^\circ$ . The faults did not pass into the sand unit above. The deformation is possibly related to slumping. Although the overlying sand unit has slumped along the present river bank, there is no conclusive evidence that the laminated sediment has slumped recently. The deformation appears to represent collapse that resulted when a supporting ice mass melted. This suggests that the sediments are ice-contact lake deposits.

Plant detritus is concentrated in sandy lenses a few mm. thick and a few dm. wide throughout the exposed laminated sediments. In approximately the upper 0.75 meter, megascopic plant remains have been largely replaced by limonite(?). Below this level plant materials are essentially unaltered, and well-preserved fossils were recovered. The lenses of whole and fragmented plant remains are interpreted as concentrations of water-logged litter that has been transported from the shore or by inflowing streams into deep water through the action of turbidity currents and deposited with silt and sand. Because these lenses occur throughout the section, having been deposited frequently over many years, they represent a common depositional phenomenon in the lake.

Leaves of the rooted aquatic *Potamogeton* occur in fine as well as coarse



laminae below the oxidized zone. Some leaves are oriented more or less vertically as if buried slowly in the position of growth. The leaf surface is commonly coated with a thin layer of calcium carbonate. These plants existed in water that was clear and warm enough to support their growth.

### PRESENT VEGETATION

Slopes on the west and east sides of the Connecticut River valley near Columbia Bridge support forest of the hemlock-northern hardwood type. Balsam fir (*Abies balsamea* (L.) Miller) and red spruce (*Picea rubens* Sarg.) occur sparsely intermixed or in more abundance on abandoned cleared land and near the summit of Monadnock Mountain. Selective logging was apparent in all visited stands except those at higher elevations. Much of the valley floor and adjacent lower slopes is nonforest land.

Moss polsters for pollen analysis were collected at four elevations on the east slope of Monadnock Mountain along the trail to its summit, and at one place on the west flank of Jordan Hill, which is southeast of Columbia Bridge (FIGURE 1). Notes were taken on forest composition around the collecting sites, but no detailed inventory was undertaken. Birches (*Betula alleghaniensis* Britton, *B. papyrifera* Marsh.) and sugar maple (*Acer saccharum* Marsh.) were frequent at all elevations except near the top of Monadnock Mountain, where balsam fir was abundant. Hemlock (*Tsuga canadensis* (L.) Carr.) and beech (*Fagus grandifolia* Ehrh.) were encountered in small amounts at low and middle elevations on the east flank of Monadnock Mountain.

Surface pollen assemblages (TABLE 1) are dominated by birch, and contributions of diverse trees and shrubs (in low percentages) account for the remainder of the arboreal component. Pollen of herbs is 9 percent or less. Fir pollen is most abundant in the sample collected just below the summit of Monadnock Mountain. Other differences in the spectra that relate to elevation are also apparent. When compared with those from surface lake muds at Brownington Pond, 47 km. to the west (Davis & Goodlett, 1960), the spectra agree in high birch and low oak values but differ in having lower percentages of beech and hemlock.

### METHODS

Samples were collected at the fossil site in October, 1976, February, 1977, and January, 1978. The lake sediments were located by digging through slumped material at the locality described and illustrated by Hollick (1931) and Lougee (1939). Because the fossiliferous sediments were near river level, we could sample them only at low water. The surface was cleaned, and, to sample as deeply as possible, a vertical pit approximately 45 × 60 cm. was dug to a depth of 1.65 meters into the lake sediments below river level. In January, 1978, a second pit was dug to 1.76 meters to recover additional material for carbon-14 analysis.

For macrofossils and for carbon-14 analysis, blocks of sediment were



TABLE 1. Pollen assemblages from moss polsters, Columbia Bridge area, upper Connecticut River valley, northern Vermont–New Hampshire.

Sample No.	1*	2*	3*	4*	5†
Elevation (meters)	955	670	455	395	410
Trees, shrubs, herbs ‡					
<i>Picea</i>	1.0%	6.0%	5.7%	8.3%	4.4%
<i>Abies</i>	12.7	2.5	2.3	3.5	2.8
<i>Pinus</i>	3.9	1.5	2.0	6.1	5.2
<i>Tsuga</i>	0.8	—	0.9	0.6	1.1
<i>Fagus</i>	1.6	0.6	1.0	1.5	1.1
<i>Acer saccharum</i>	3.2	4.5	2.2	14.1	5.1
<i>Fraxinus</i> 4-colpate	1.8	0.4	0.3	0.1	1.7
<i>Juglans</i>	—	—	0.1	—	—
<i>Carya</i>	—	0.1	—	—	—
<i>Quercus</i>	3.4	1.2	2.0	1.0	1.0
<i>Ulmus</i>	1.6	0.1	0.1	0.4	0.2
<i>Fraxinus</i> 3-colpate	0.5	—	0.2	0.2	1.2
<i>Acer rubrum</i>	0.5	0.6	0.3	0.1	1.2
<i>Betula</i>	58.9	72.5	62.6	50.3	65.7
<i>Carpinus-Ostrya</i>	0.3	0.4	—	1.5	0.1
<i>Populus</i>	—	0.1	—	0.1	—
<i>Juniperus-Thuja</i>	—	—	0.1	0.4	0.3
<i>Alnus</i>	1.1	0.7	0.7	0.8	0.9
<i>Salix</i>	0.2	—	0.1	0.1	0.1
<i>Acer spicatum</i>	0.5	4.9	14.4	1.4	0.6
<i>Corylus</i>	0.2	—	—	0.1	0.1
Cyperaceae	0.2	0.1	—	—	—
Gramineae	1.0	0.8	1.4	4.8	2.5
<i>Ambrosia</i>	6.1	1.3	2.4	3.6	3.1
<i>Rumex</i>	—	0.1	—	0.1	0.3
<i>Plantago</i>	—	0.4	0.1	—	—
Chenopodiaceae-					
Amaranthaceae	0.2	—	—	0.1	0.4
High-spine Compositae	0.3	0.4	0.8	0.3	0.7
<i>Ranunculus</i>	0.2	0.1	—	—	—
<i>Coptis</i>	—	—	0.1	—	—
Sum AP	92.1	96.4	95.2	91.0	92.9
Sum NAP	7.9	3.6	4.8	9.0	7.1
Miscellaneous §					
Polypodiaceae	27.7	12.2	8.7	10.5	33.0
Lycopodiaceae	0.2	0.2	—	0.1	0.6
Osmundaceae	—	—	—	0.1	—
Ophioglossaceae	0.1	0.1	—	—	—
<i>Typha-Sparganium</i>	—	—	—	0.2	—
Broken Abietineae	2.3	0.8	1.4	1.4	1.7
Unfamiliar	0.1	0.1	—	0.3	0.1
Unknown	1.9	1.5	5.7	2.2	2.2

\* Samples from east slope of Monadnock Mountain, Essex County, Vermont.

† Sample from west slope of Jordan Hill, Coös County, New Hampshire.

‡ Percentage base = sum AP + NAP.

§ Percentage base = sum AP + NAP + sum miscellaneous.



cut from the pit at those levels where lenses of organic detritus were concentrated. These were wrapped in aluminum foil for transport. In the laboratory the blocks were teased apart, and plant-bearing horizons were washed with tap water through a 500  $\mu$ m. sieve. Residues were examined under a dissecting microscope. For two of the carbon-14 analyses (WIS-919 and WIS-961), detrital wood fragments (ca. 4.5 g. dry weight) were picked from the residues under a dissecting microscope. For WIS-925, a sediment block rich in organic detritus was submitted. Carbon-14 analyses were made by the Radiocarbon Laboratory, Center for Climatic Research, University of Wisconsin, Madison.

Sediment samples for pollen analysis were cut from a fresh vertical wall of the pit in 5 cm. lengths of triangular cross section (ca. 5 cm. along a side). In the laboratory a 4 cc. subsample was removed from across the full length of selected segments after the exposed sediment had first been chipped away. In an unsuccessful attempt to determine total depth by augering and probing, the laminated sediment was penetrated to 3.59 meters. Sediments between 3.49 and 3.59 meters were collected in a Davis sampler head. Subsamples from this short core, which was 1.89 meters below the next sample above, were combined for pollen analysis.

Subsamples were macerated in 10 percent hydrochloric acid and 70 percent hydrofluoric acid, and the residues were sieved followed by flotation in zinc chloride solution (sp. gr. 2.0). Residues with excessive organic matter were acetolyzed. Glycerine jelly was the mounting medium.

Concentrating the pollen and spores, which occurred in low densities in the sediments, was facilitated by washing extraneous materials through a screen with 10  $\mu$ m. openings. Unsieved residues were diluted with large amounts of fine silt- and clay-sized particles that made tabulation of the pollen and spores time-consuming and impractical. Fine-grained, insoluble, opaque particles of unknown composition were especially troublesome. Nitex Monofilament Nylon Screen HC (high capacity) 3-10 (available from TETKO, Inc., Elmsford, New York 10523) was used. After treating a sample with acids, the residue was washed with distilled water through the screen. The sieving apparatus consisted of a cylindrical plastic freezer container with the flat bottom and all but the rim of the lid cut away. A square piece of screen was placed over the top of the container and clamped tightly in place with the lid-rim, which extended above the taut screen. A residue was washed onto the screen after the apparatus was suspended by its rim in a beaker. The complete apparatus was vibrated on an electromagnetic sieve shaker, and water was added from a wash bottle until only clean water moved through the screen. The screen was then removed, and the residue was washed into a beaker with repeated jets from a wash bottle. The screen was examined under a microscope for adhering particles and, if necessary, washed again. The residue was concentrated by centrifuging. No pollen grains were detected in the sediment that passed through the screen. Also, a few unscreened samples were laboriously counted and compared with spectra from screened duplicate samples. Pollen assemblages obtained from the same depth by both methods were similar, and we concluded that little, if any, pollen found its



way through the screen. We were able to recover pollen in concentrations of less than 100 grains per cc. of sediment.

For determination of pollen concentration, separate subsamples, each consisting of 2.5 cc. of sediment from across a single rhythmite, were taken at evenly spaced intervals through the section. The moist sediment was measured by pressing it into a 1.25 cc. measuring spoon. These subsamples were treated like the others (although none was acetolyzed), and the residues were placed in glycerine jelly. A residue-fraction was determined by first counting the number of drops of liquid glycerine jelly containing the residue, then placing one or two drops on a microscope slide after completely mixing the residue with a pumping action of the pipette and bulb. If it is assumed that each rhythmite is a yearly increment, then the number of pollen and spores per cubic centimeter (total number in a residue divided by 2.5) multiplied by the varve thickness equals the number of pollen and spores deposited per cm.<sup>2</sup> per year (i.e., pollen influx).

The residues were counted at a magnification of 200 $\times$ . Microscope slides were traversed according to a prescribed plan to prevent overlap and insure randomness. Except where density was too low, each sample was counted until a sum of 300 arboreal and shrub pollen grains was reached. A collection of modern pollen consisting of about 10,000 slides and broadly representing the flora of North America was routinely used for reference purposes. Pollen of *Dryas Drummondii* Richardson, a species represented in the deposit by abundant macrofossils, proved upon careful examination to be different from that of other *Dryas* species. It sometimes appeared scabrate (pollen grains were in various stages of development on the reference slides) and with no alignment of elements to produce rugulae or striae. Thus, especially when slightly degraded, pollen of *D. Drummondii* can appear much like that of *Quercus*. However, after re-checking all grains doubtfully identified as *Quercus*, we found only one or possibly two that we concluded might be of *D. Drummondii*.

To measure the present-day pollen rain in the vicinity of the fossil site, several samples of moss polsters were analyzed. Tips of the moss plants were cut off and acetolyzed, and the residues were sieved through fine metal screening. The pollen residues were counted like the others.

Both fossil and modern seeds received two coatings of gold-palladium (total thickness 250 Å), preceded by an optional coating of carbon, prior to examination with a scanning electron microscope (AMR Model 1000). Fully mature seeds of representative form were selected for SEM study after examination of seeds from at least two different herbarium specimens of each species.

## RESULTS

### POLLEN ANALYSES

Except for minor pollen and spore types, which are listed in APPENDIX A, results of the pollen analysis are displayed in FIGURE 2. The scale at the left of the diagram represents depth below the top of the laminated



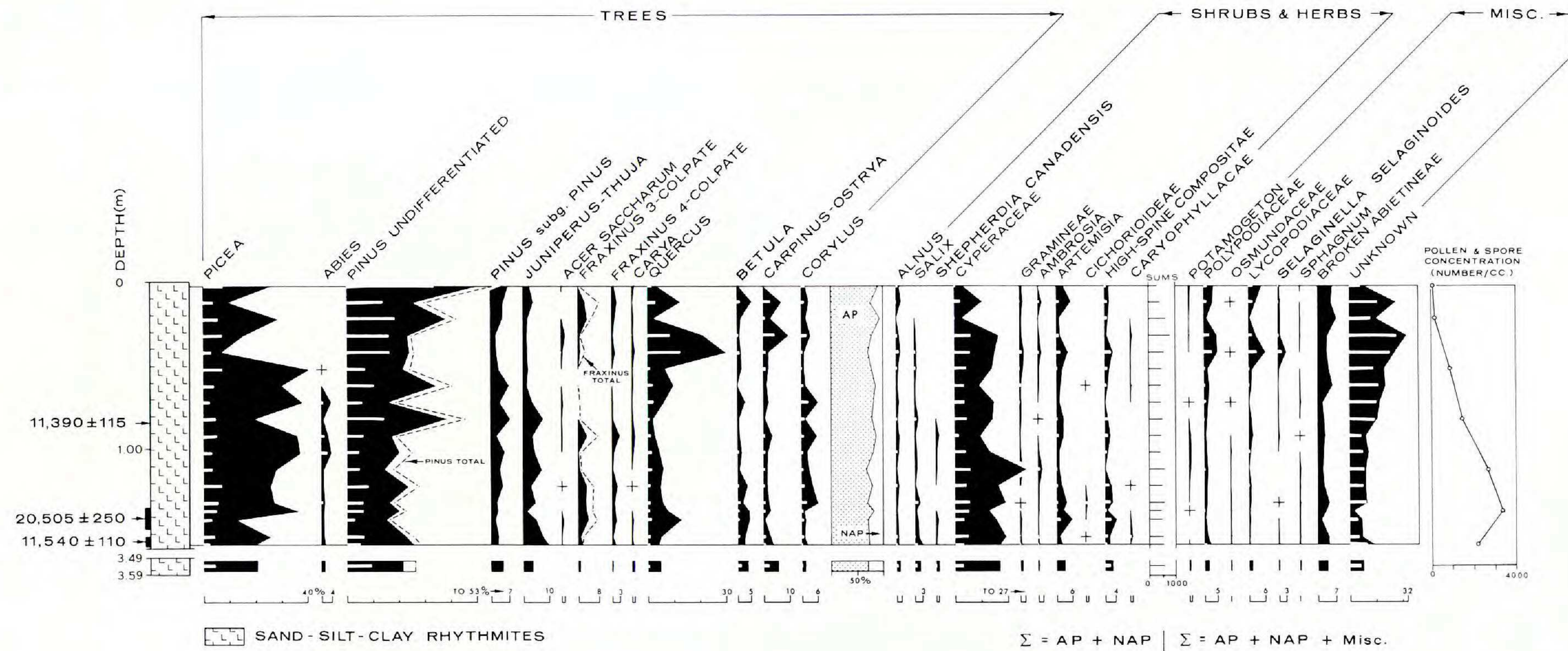


FIGURE 2. Pollen diagram. White bars within silhouettes represent percent deteriorated grains in any category. Most unknown grains too badly preserved to permit more precise identification.



sediments. The three carbon-14 age determinations are next to bars or marks that represent depths from which the analyzed samples were taken. Deteriorated pollen (Cushing, 1964) occurred at all sampled levels, and the white bars within the silhouettes represent percent deteriorated in any category. Percentages of trees, shrubs, and herbs are based on the total number of pollen grains of arboreal and nonarboreal plants at any one level excluding those categories designated miscellaneous. The percentage base for the miscellaneous category is the sum of all items at a given level.

Some pollen types have been subdivided on the basis of morphological characters, as is common in modern pollen analysis. Pollen of *Picea* was not further divided because size and cap thicknesses overlapped too much to allow any subgroups to be distinguished. Of the three curves representing pine pollen, *Pinus* subg. PINUS includes pollen with an observable psilate germinal furrow. No grains with verrucose furrow surfaces (the *Pinus* subg. STROBUS type) were observed. Undifferentiated *Pinus* includes pine pollen in which sculpturing of the distal face could not be seen. Total *Pinus* represents the sum of the two categories, including corroded grains. No deteriorated *Juniperus-Thuja* pollen was recognized. With slight deterioration of this pollen type, the granules are probably destroyed, resulting in a smooth, nondiagnostic, inaperturate body. The *Fraxinus*-total curve is the sum of *Fraxinus* 3- and 4-colpate plus the percentage of deteriorated *Fraxinus*. Deteriorated *Fraxinus* pollen was not divided into 3- and 4-colpate types and is not represented by white bars in the diagram. We interpret 3-colpate *Fraxinus* to be *F. nigra* Marsh.; those with four colpi are other species including *F. americana* L., *F. pennsylvanica* Marsh., and *F. quadrangulata* Michaux.

Pollen and spores in the unknown category were not identifiable for one of the following reasons: deterioration was so great that they were recognized as spores or pollen grains only; preservation was good, but the form was unfamiliar — therefore they could not be assigned to any known family or lower taxon; preservation was good, but the microfossil was folded or obscured by debris, thereby hiding diagnostic features. Unknown microfossils were nearly all badly deteriorated.

Although the sampled sediments probably represent only a few hundred years, percentages of the various recognized pollen and spore types show prominent fluctuations that signal possible ways to subdivide the pollen diagram into zones. However, as will be discussed later, the most important pattern appears related to the sediments being oxidized above 0.75 meter. Below this level *Abies* is uniformly present, *Juniperus-Thuja* is better represented, and increased *Picea* and decreased *Pinus* percentages are apparent. Also in the topmost layers, the percentage of unknown (i.e., mostly deteriorated) microfossils is greatest, and pollen and spore concentration is lowest.

Spectra from unoxidized sediment below 0.75 meter are more reliable indicators of the original unaltered pollen assemblages. About 75 percent of a spectrum below 0.75 meter consists of tree pollen types, with *Picea* and *Pinus* predominating. Most of the pine pollen is of the subg. PINUS



type, which includes *Pinus Banksiana* Lamb. and *P. resinosa* Aiton. Pollen of various deciduous genera of trees or shrubs (*Acer*, *Betula*, *Carpinus* and/or *Ostrya*, *Carya*, *Corylus*, and *Fraxinus*) is present, but percentages of *Acer* and *Carya* are low, and about 10 percent or less each of *Fraxinus* and *Quercus* is present. Pollen from nonarboreal sources (mostly of Cyperaceae) comprises 25–30 percent of the spectra. *Artemisia* and other Compositae are also relatively well represented. Our counts included no pollen of the arctic and alpine herbs that characterize late glacial sediments in southern Quebec (Richard, 1977). The average of four pollen and spore concentration determinations below 0.75 meter is 2435 microfossils per cc.

#### MACROFOSSILS

Unoxidized megascopic plant fossils occurred mainly between 1.38 and 1.45 meters, and this interval yielded the material upon which the following descriptions are based. Intact specimens were impossible to obtain from the oxidized upper 0.75 meter of sediment, where fossils were too fragile to be freed from the matrix by wet sieving. A continuous record was not obtained below 0.75 meter because organic layers were not always present along the vertical sampling line. Nevertheless, only one macrofossil assemblage appears to be present between 0 meters and the level of the lowest radiocarbon date. The topmost 0.75 meter of sediment, where preservation was poorest, contained several concentrations of limonitic (rust-colored) leaves resting parallel to the bedding planes. Although lacking in morphological detail, all leaf-types found above 0.75 meter are also represented in unoxidized sediments below this level. Similarly, in the nearly 0.5 liter of wet sieve residue that produced wood fragments used for radiocarbon dating the interval 1.52–1.58 meters, no kind of plant fossil was encountered that did not also occur between 1.38 and 1.45 meters.

Species were identified with the aid of an herbarium-vouchered collection of seeds, fruits, and other plant organs that includes all northern species of an identified genus listed in Fernald (1950), as well as all species recognized by Polunin (1940) for the Canadian eastern Arctic and by Scoggan (1950) for the Gaspé Peninsula, Quebec. Because some plants represented in the deposit are characteristic of northwestern North America, particularly western Canada, the listing of Canadian seed plants by Boivin (1966–67) was used as a basis for expanded coverage. In some cases a special effort was made to compare the fossils with species and varieties known exclusively from western America, but the absence of suitable herbarium material and the existence of unsettled taxonomic problems in certain genera made this difficult to do in all cases. Our work on the Columbia Bridge fossils indicates that species of western North America should be considered when identifying late glacial plant fossils from sites in eastern (and probably central) temperate North America.

The brief morphological and taxonomic notes that follow are presented



as partial documentation of the identifications. In some cases more extended discussions are found in APPENDIX B. Ranges are mostly from Fernald (1950) and Hultén (1968) and include only a New World segment of a distribution that may be amphiatlantic or completely or partly circumpolar. Species concepts generally follow Fernald (1950). For infrequent and rare fossils, we give the number of specimens recovered, but these figures are only a general indication of abundance. They are based on the number of intact fossils recovered from about 1.5 liters of wet sieve residue, which was comprised mostly of degraded and unidentifiable plant material. The number of recovered intact fossils probably does not accurately reflect vegetation composition.

**Equisetum** sp. Three aerial stem fragments (stomata visible), including nodes with whorled leaves, chartaceous leaf tips worn away; one rhizome fragment. In size the specimens agree best with *E. pratense* Ehrh., *E. scirpoides* Michaux, and *E. variegatum* Schleicher, all of which are northern and transcontinental in distribution, although small specimens of other species, such as *E. arvense* L., are also similar. Unfortunately, cortical tissues and the system of internal canals, which provide characters of taxonomic value, are absent in the specimens.

**Selaginella selaginoides** (L.) Link. Two megaspores; also microspores (see FIGURE 2). Megaspores of *S. selaginoides* are finely punctate; those of *S. apoda* (L.) Fern. and *S. rupestris* (L.) Spring are reticulate. A species of calcareous habitats, and in North America the most northern of the three species, *S. selaginoides* occurs from Greenland and Labrador to Alaska, and, in the East, south to northern Maine and the upper Great Lakes region.

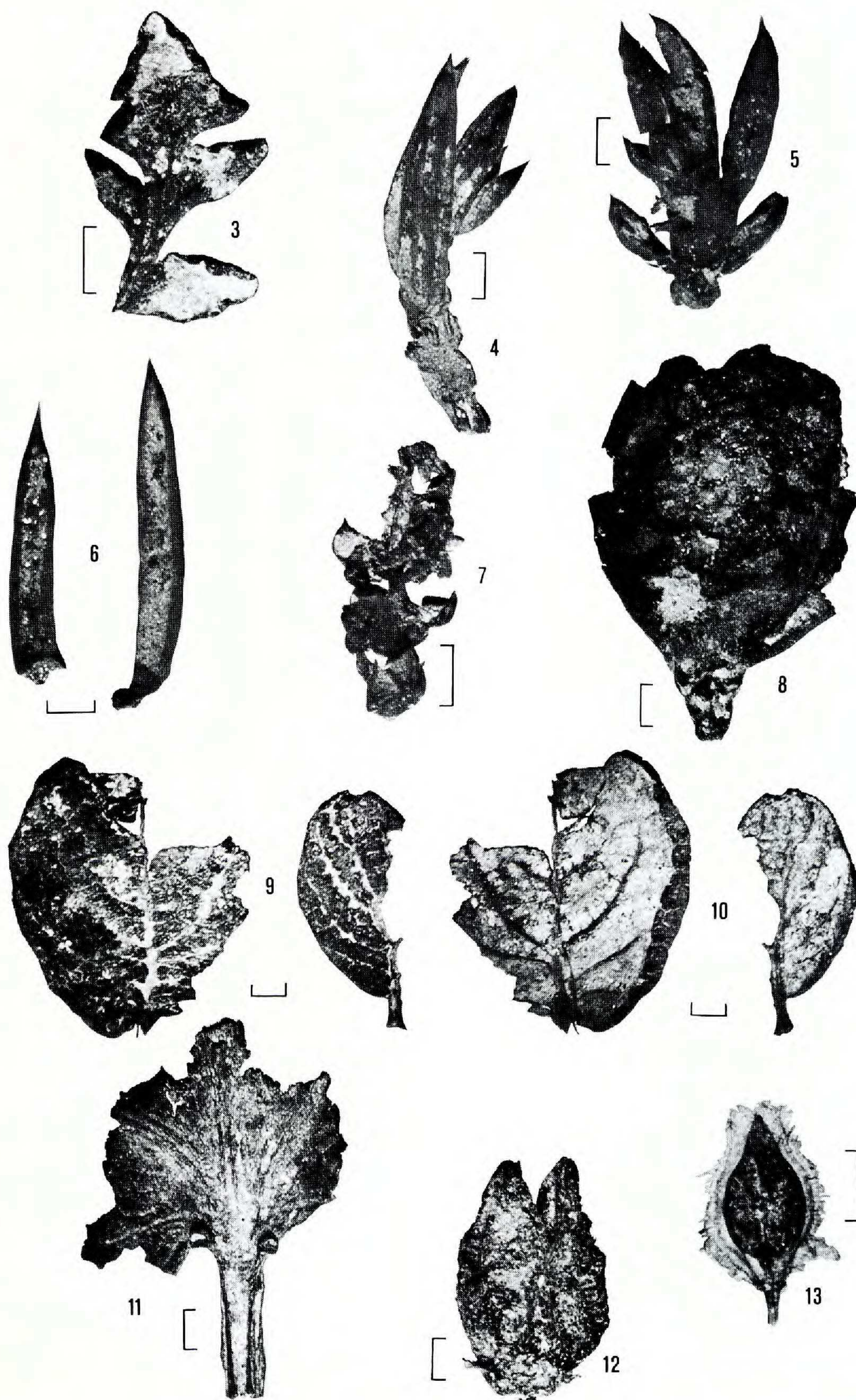
**Woodsia ilvensis** (L.) R. Br. A pinna, margins revolute, with dorsal uniseriate trichomes. In other northern species of *Woodsia*, leaf margins are plane to weakly revolute, or fronds are glabrous or have conspicuous glandular trichomes. Scales, which arise from the underside of fronds of *W. ilvensis*, were not seen in the fossil. The species occurs in exposed, rocky habitats from the eastern Arctic, south to Pennsylvania and North Carolina (uplands only), and west to Alaska and British Columbia. FIGURE 3.

**Picea** sp. Ten well-preserved needles and one cone scale (5 mm. long, 4 mm. wide), with the wings of both seeds visible. The scale is wedge shaped, and its dorsal surface is divided into a distal smooth portion

---

FIGURES 3–13. Plant macrofossils from Columbia Bridge site. 3, *Woodsia ilvensis*: pinna, lower surface. 4–8, *Juniperus communis*: 4, 5, branch tips; 6, isolated needles; 7, microsporangiate cone; 8, fleshy, ovulate cone. 9, 10, *Salix vestita*, two leaves: 9, upper surfaces; 10, lower surfaces. 11, 12, *Populus balsamifera*: 11, leaf fragment, glands at both sides of petiole apex; 12, capsule, note basal disc. 13, *Oxyria digyna*: fruit, outer parts of wing absent. Scale lines = 1 mm.







(umbo) and a proximal area of different texture. These features rule out *Abies*, *Larix*, *Pinus*, and *Thuja*. Macrofossils of spruce are poorly represented in the deposit, but at least some reproducing individuals grew near the site.

***Juniperus communis* L.** Twenty-one isolated needles, seventeen branch tips with attached needles, two fleshy ovulate cones, two seeds, and one microsporangiate cone. Mean needle length ( $n = 21$ ) is 6.1 mm.; ovulate cones measured 8 and 5 mm. wide. Of the several varieties of *J. communis* recognized by Fernald (1950), the fossil needles are too short for vars. *communis* and *depressa* Pursh, while the ovulate cones are too small for var. *megistocarpa* Fern. The fossils best match var. *saxatilis* Pallas, which grows in exposed places from Greenland to Alaska, and in the East as far south as the mountains of northern Maine. FIGURES 4–8.

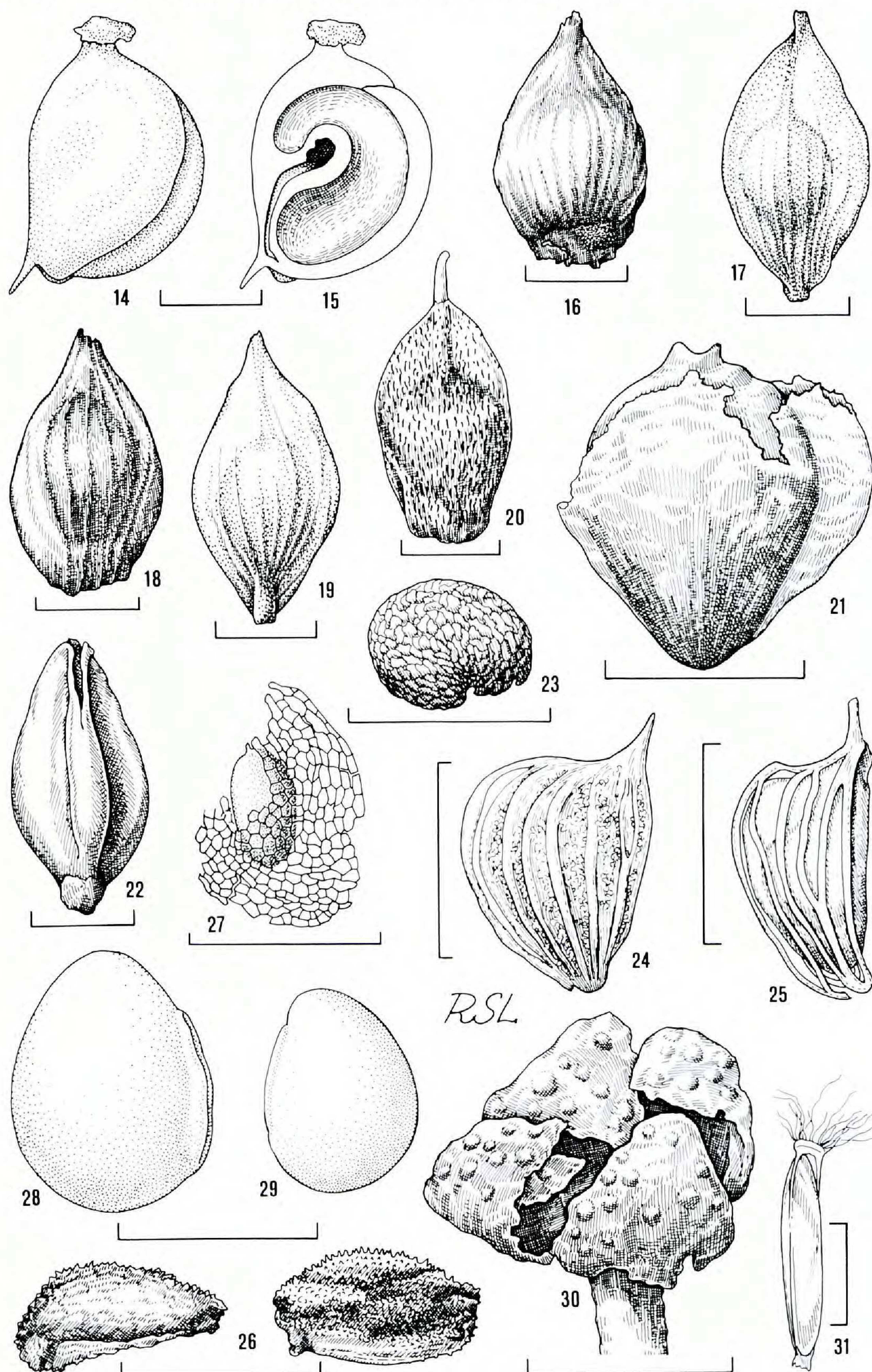
***Potamogeton filiformis* Pers.** Twenty-seven endocarps, some with portions of the exocarp still adherent, indicating the absence of a lengthy period of predepositional transport. Identification of pondweed fruits is facilitated by the works of Aalto (1970), Jessen (1955), and Martin (1951). Diagnostic fruit characters of *P. filiformis* include size (ca. 2.5 mm. long, 2 mm. wide) and a rounded lid (crest present in fruits with exocarps intact) that ends well below the style, which is more or less centrally placed as opposed to being nearer the ventral side as in the similar *P. vaginatus* Turcz. Aalto (1970) indicated that the base of the lid does not taper in *P. filiformis*, while it is V shaped in *P. vaginatus*, but this distinction does not appear to hold for the North American material that we studied of these species. Based in part on size measurements given by Martin (1951), which are in general larger than those of Aalto (1970), we have identified the specimens as *P. filiformis*, a species of calcareous, sometimes brackish waters from Greenland to Alaska and southward sporadically to northern New England, Minnesota, and Nevada. FIGURES 14, 15.

***Potamogeton pusillus* L.** One endocarp. Fruits of this pondweed are small (2 mm. long, 1.5 mm. wide) and have an S-shaped ventral margin and a convex lid that extends to the style base. The species occurs in cal-

---

FIGURES 14–31. Plant macrofossils from Columbia Bridge site. 14, 15, *Potamogeton filiformis*: 14, lateral view of endocarp, stigma at top; 15, endocarp in longitudinal section showing embryo cavity and lid apex, which ends well below style. 16–19, *Carex bipartita*: 16, fossil, ventral side of perigynium (achene in place); 17, fruit from herbarium specimen, same view; 18, same fossil, dorsal side of perigynium; 19, fruit from herbarium specimen, same view (17, 19, from Canada, Newfoundland, hills east of Little Quirpon Harbour, Fernald & Gilbert 27622, 8 Aug. 1925 (GH)). 20, *Carex aquatilis*: perigynium, achene in place. 21, *Betula* cf. *glandulosa*: winged fruit. 22, *Polygonum ramosissimum* cf. var. *prolificum*: achene with fragment of calyx adherent at base. 23, *Arenaria* cf. *dawsonensis*: seed. 24, 25, *Ranunculus Cymbalaria*: two achenes. 26, *Saxifraga aizoides*, seeds: right, fossil; left, from herbarium specimen (Canada, Québec, Gaspé Peninsula, bluffs and slopes, Bonaventure River, Collins et al. 5222, 5, 6,





& 8 Aug. 1904 (GH)). 27, *Parnassia* cf. *Kotzebuei*: seed, cellular testa partly broken away. 28, *Sibbaldia procumbens*: achene. 29, *Potentilla* sp.: achene. 30, *Shepherdia canadensis*: staminate flower. 31, unknown composite: achene. Scale lines = 1 mm.



careous waters from Gaspé County, Quebec, to northern Alberta, and in eastern North America south to Louisiana and Texas.

Both *P. filiformis* and *P. pusillus* have narrow leaves (less than 1 mm. and to 3 mm. wide, respectively). Much wider *Potamogeton* leaves were reported by Hollick (1931) from the Columbia Bridge beds. These are similar to leaves (ca. 1 cm. wide) we also observed at many places in the lower part of the section. Their specific identity is unknown.

**Carex bipartita** Bellardi ex All. One perigynium, achene in place. Although the base and apex of the perigynium are imperfectly preserved, the fruit belongs to sect. HELEONASTES Kunth because of its rounded, wingless margins, short beak, and lenticular achene. The fossil compares well in size and shape with *C. brunnescens* (Pers.) Poiret but lacks the serrulate beak of that species. In all important features it matches fruits of *C. bipartita*, a sedge of subarctic and arctic regions from Greenland to Alaska, south to the mountains of the Gaspé Peninsula, Quebec, in the East, and to Colorado and Utah in the West (Hermann, 1970). It is a calcicole on the Gaspé Peninsula (Scoggan, 1950). In the Arctic the species grows on moist to wet sand and turfy places near streams and lakes or on hillsides (Polunin, 1940; Porsild, 1964). FIGURES 16–19.

**Carex aquatilis** Wahlenb. Five perigynia with achenes. The perigynia are biconvex, and the achenes, which are visible with transmitted light, lack a lateral constriction and do not fill the perigynium apex. These are features of *Carex* sect. ACUTAE, and, of possible species in this section, the fossils agree best with the variable *C. aquatilis*. Linear groups of red-pigmented cells are present in a few of the perigynia. Similar punctulae are evident in some herbarium specimens of the species. A sedge of wet sites (shallow pools, pond margins, river banks, and wet meadows), the species ranges from Greenland to Alaska, south to Quebec, northern Michigan, Arizona, and California (Hermann, 1970). FIGURE 20.

Sedge achenes are the most abundant seed- and fruit-type in the deposit. Species other than those listed above are represented as judged from the different sizes and shapes of both lenticular and trigonous types among the 85 sedge achenes recovered from the sieve residues. No attempt has been made to identify these.

**Salix vestita** Pursh. Seventeen leaf fragments, five of which include petioles. The leaves are obovate or elliptic and have rugose upper surfaces, pubescent undersides, and revolute margins. Hollick (1931) listed *S. reticulata* L. as a member of the Columbia Bridge flora, but to judge from published photographs of fossils so named, his specimens could be *S. vestita*. In our carbonized and fragmented but otherwise unaltered fossils, small resinous glands occur on the petiole margins and at the edges of the leaves near the petiole. Such glands do not occur in *S. reticulata* but appear diagnostic for *S. vestita*. An ascending shrub of calcareous soils in boreal and subarctic areas from Newfoundland and Labrador to northern and eastern Quebec, *S. vestita* also occurs disjunctively westward in north-



western Ontario and adjacent Manitoba, in the mountains along the border between southern Alberta and British Columbia, and at a few places in the northwestern United States (FIGURE 69). George W. Argus, a specialist on American willows, has confirmed the identification. FIGURES 9, 10.

*Salix* cf.<sup>2</sup> *Uva-ursi* Pursh. Fragmentary leaves, one a complete leaf base with veins that run parallel to the margin (which is entire, as is usual for leaves borne lower on shoots of this willow; G. Argus, *in litt.*), and three fragments with marginal teeth that are too widely spaced to compare well with those of *S. herbacea* L. Leaves of *S. Uva-ursi* vary from elliptic to obovate, with the apex acute to obtuse, the base attenuate, and the margins dentate, crenulate, or subentire to entire. Leaves of *S. herbacea* are widely elliptic, with the apex usually obtuse or retuse and the base more or less cordate. Capsules recovered from the deposit ( $n = 37$ ) are glabrous, have tapered beaks of moderate length, and also match those of *S. Uva-ursi* in size. *Salix Uva-ursi* is a willow of the eastern North American Arctic (Greenland to the east coast of Hudson Bay) that occurs southward to the alpine areas of Quebec and northern New England, and New York.

*Salix* cf. *argyrocarpa* Andersson or *S.* cf. *pellita* Andersson. Fifteen leaves and fragments, none over 1 cm. in length, and five fragments with petioles and part of the leaf blade; margins entire in all specimens. The fossil leaves are narrowly elliptic, attenuate, and strongly revolute at the base, and have a deep groove on the adaxial face of the petiole. Young leaves of *S. pellita* are similar in shape to mature leaves of *S. argyrocarpa*, although fully developed leaves of the former can be 10 cm. or more in length. Leaves of both species may have entire or crenulate margins. While the recovered fragments are all small, complete limonitic leaves of similar shape but larger size (to 4 cm.) were found in the upper, oxidized part of the deposit. These match herbarium material of *S. pellita*, but a positive identification is not possible. *Salix argyrocarpa*, a shrub of moist alpine or subalpine meadows, occurs from Labrador south to northern New Hampshire; *S. pellita*, which has a similar range (southern Labrador south to northern New England and Michigan), usually does not grow at higher elevations.

Both species were listed by Hollick (1931), but neither the limonitic leaves available to him nor the newly collected carbonized fragments, in our opinion, present sufficient characters for unequivocal identification.

*Populus balsamifera* L. Abundant material including limonitic leaves, a carbonized leaf base and petiole, bud scales, six capsules or capsule valves, and seeds of a *Populus*, probably of *P. balsamifera*. Hollick (1931) identified limonitic leaf fossils of similar appearance as *P. balsamifera* and *Celtis occidentalis*. However, we can find no consistent differences between

<sup>2</sup> The designation "cf." means that the fossil compares well with recently collected material of the species, but for some reason a conclusive identification cannot be made.



his illustrations of fossils given these names and suggest that material referred to *Celtis* is, in fact, *P. balsamifera*. No fossils of *Celtis* were found by us, and, in their absence, as well as for ecological reasons, it seems justifiable to drop from the flora *C. occidentalis*, a species now rarely found north of southern New England.

Capsules of *Populus* have a basal disc (FIGURE 12), while those of most willows (species of sect. RETICULATAE Fries excepted) lack this character. Capsules of *P. balsamifera* are large (to 8 mm. long) and strongly rugose; those of *P. grandidentata* Michaux and *P. tremuloides* Michaux are smaller and less rugose; those of *P. deltoides* are larger and do not taper to a prominent beak. The fossil seeds are narrowly oblong (2 mm. long, 1 mm. wide) and have a short apical point and an obtuse base. The fossil bud scales are mostly long (to 1.5 cm.), black, and resinous and compare well with bud scales of *P. balsamifera* and *P. deltoides*. The leaf base illustrated in FIGURE 11 is probably of *P. balsamifera*, although similar glands occur near the petiole apex in other poplars. (They are especially prominent in leaves of *P. deltoides* but are not present on all leaves of *P. balsamifera* and are inconspicuous in herbarium specimens of *P. grandidentata* and *P. tremuloides*.) Glands resembling those illustrated are found at the petiole apex in *Viburnum edule* (Michaux) Raf. and *V. trilobum* Marsh., but in *Viburnum* the glands are stalked and usually somewhat foliar.

Except in northern United States and southern Canada, where the species occurs in the coniferous-hardwood zone, the range of *Populus balsamifera* mostly coincides with the transcontinental boreal forest region. In the East it extends southward to northern New England and New York (sporadically beyond), and to Michigan, northern Wisconsin, and Minnesota. It is a pioneer along streams and rivers and in other disturbed situations. FIGURES 11, 12.

**Betula cf. glandulosa** Michaux. One fruit, wings poorly preserved. Birch fruits differ in size, width and shape of the wings, and size and shape of the central seed. Based on its size ( $2 \times 2$  mm.), its narrow wings, which are broader toward the apex, and its wedge-shaped seed base, the fossil is probably *B. glandulosa*. Fruits of *B. pumila* are sometimes slightly larger (3 mm. wide, 2 mm. high) and generally have somewhat broader wings; those of *B. nana*, which Hultén (1968) maps as being transcontinental across the Canadian Low Arctic, are the same size as those of *B. glandulosa* and in at least some specimens have wings about half as broad as the central body. Mature carpellate cone bracts of the three species are also usually similar in size and shape, and the resinous hump on the back of bracts of *B. glandulosa* (Hultén, 1968) may or may not persist during fossilization. Examination of collections in the combined herbaria of the Arnold Arboretum and Gray Herbarium indicates that fruit and carpellate cone bract characters may not be diagnostic for *B. glandulosa*, *B. nana*, and *B. pumila*. As interpreted by Hultén (1968), *B. glandulosa* occurs across boreal North America (but extending farther south than *B. nana*) from Greenland to Alaska, and in the East southward to alpine areas of



Quebec, Maine, New Hampshire, and New York. *Betula pumila* is a plant of bogs and wooded swamps from Newfoundland to British Columbia, and south sporadically to the northern United States. FIGURE 21.

*Oxyria digyna* (L.) Hill. One fruit, peripheral parts of wing absent, achene lenticular. An arctic-alpine species that is known in eastern North America as far south as the mountains of the Gaspé Peninsula and northern New Hampshire. FIGURE 13.

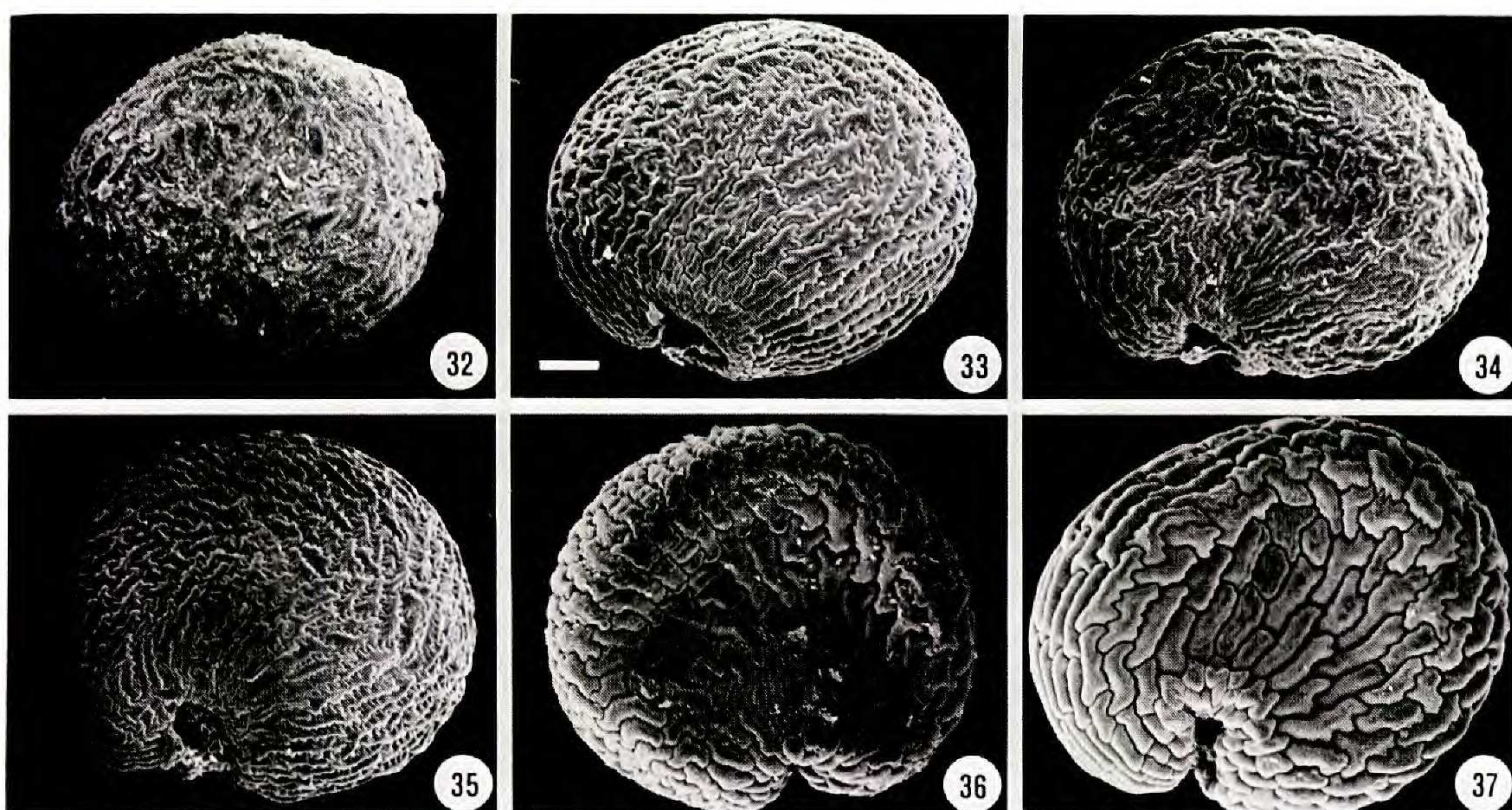
*Polygonum ramosissimum* Michaux cf. var. *prolificum* Small (*P. prolificum* (Small) B. Robinson). Four achenes, calyx base persisting in fossils. Identification is based on the triangular (and 3-angled) shape of the achenes, whose concave sides lack pits or punctae. The fossils are similar in shape to achenes of *P. buxiforme* Small (*P. aviculare* var. *littorale* (Link) W. D. J. Koch; see Mitchell & Dean, 1978) but differ from fruits of this species in lacking punctae. The identity of the fossil material was suggested by R. S. Mitchell. *Polygonum ramosissimum* is a plant of sandy and light soils along shores and in disturbed habitats (roadsides) in temperate areas of North America (New England and southwestern Quebec to Washington, and south to Pennsylvania and Texas); var. *prolificum* has a similar range. FIGURE 22.

*Arenaria* cf. *dawsonensis* Britton. One seed. The identity of the fossil is uncertain because of somewhat poor preservation and sediment-obscured intercellular areas, which do not allow a satisfactory match with herbarium reference specimens. *Arenaria dawsonensis* is distributed westward from southern Labrador and Newfoundland to Yukon and Alberta, and in the East as far south as eastern Quebec. It is a plant of calcareous ledges and gravel. See APPENDIX B. FIGURES 23, 32, 33.

*Silene acaulis* var. *exscapa* (All.) DC. One seed, cells of seed coat black and bulging, anticlinal walls of seed coat cells strongly undulate. Although the testa is somewhat abraded and obscured by small sediment particles, the fossil fits within the variation observed in seed samples of New World populations of *S. acaulis* (FIGURES 39–41). The distorted part of the seed coat near the hilum (FIGURE 38) is where the radicle emerges at germination; thus the fossil may be of a germinated seed. *Silene acaulis* var. *exscapa* occurs across subarctic and arctic America, and in the East it is found south to alpine areas of Quebec and New Hampshire. FIGURES 38–41.

*Ranunculus Cymbalaria* Pursh. Two achenes. Fruits of species of *Ranunculus* are smooth, pitted, punctate, or longitudinally (*R. Cymbalaria* only) or transversely ribbed. Longitudinally ribbed fruits of species of *Thalictrum* (e.g., *T. alpinum* L.) differ from those of *R. Cymbalaria* in shape and in the more centrally placed style. *Ranunculus Cymbalaria* is distributed across northern North America from southern Greenland to Alaska, and south to New Jersey and Arkansas in the East. FIGURES 24, 25.



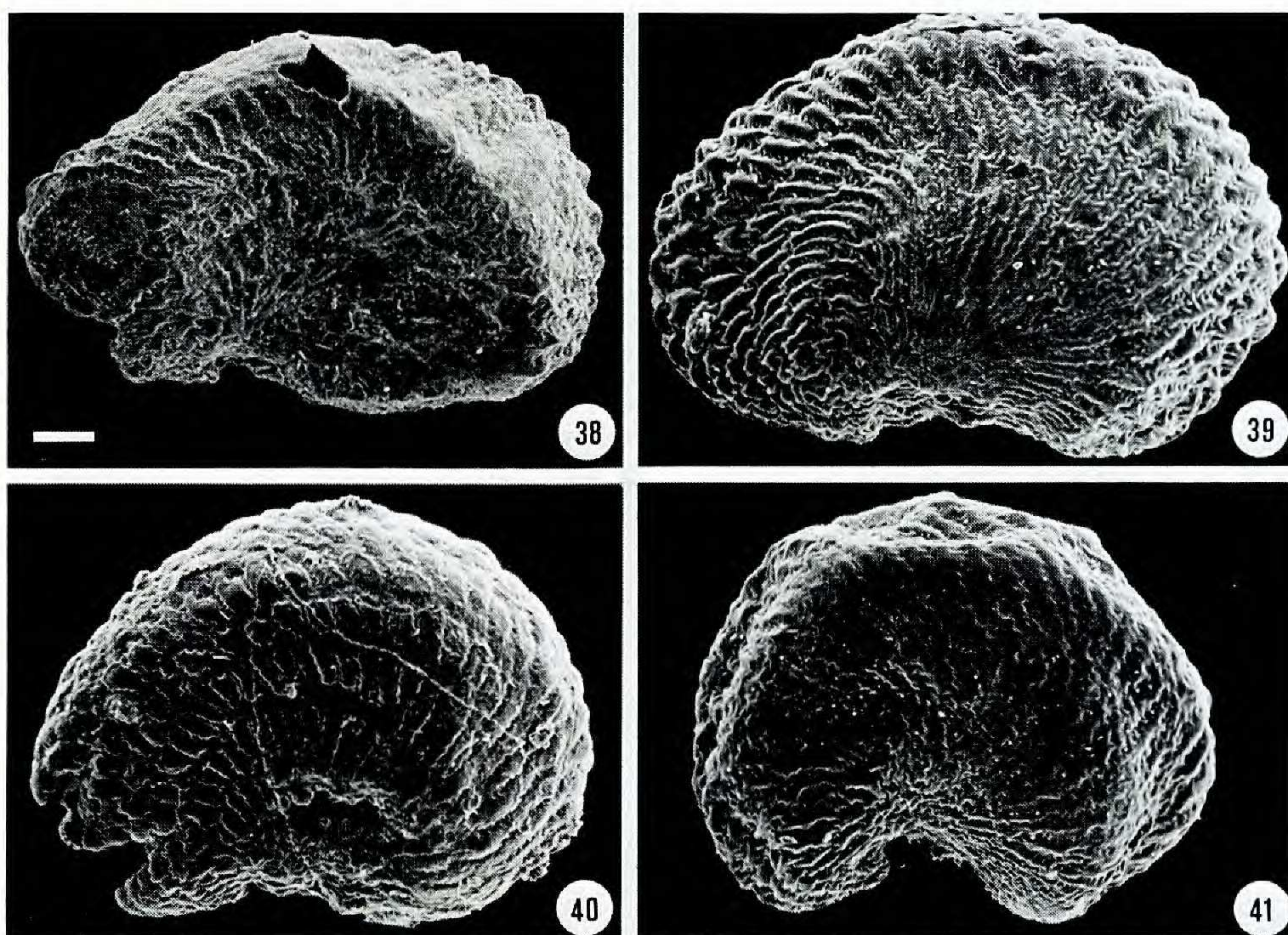


FIGURES 32–37. Scanning electron micrographs, seeds of species of *Arenaria*: 32, *A. cf. dawsonensis*, fossil seed, sediment particles visible on surface; 33, *A. dawsonensis* (Canada, Newfoundland, Mt. Musgrove and Humber Mouth, *Fernald & Wiegand* 3355, 18 July 1910 (GH)); 34, *A. uliginosa* Schleicher in Lam. & DC. (*A. stricta* Michaux s. l., *fide* Boivin, 1966–67) (Canada, N.W.T., Smith Arm, Great Bear Lake, *Porsild & Porsild* 5077, 16–21 July 1928 (GH)); 35, *A. Rossii* (Canada, N.W.T., South Bay, Southampton Island, *Polunin* 2282, 22 Aug. 1936 (GH)); 36, *A. patula* (U.S.A., Kentucky, Mundy's Landing, *Wharton* 8914 25 May 1955 (GH)); 37, *A. stricta* (U.S.A., New York, Essex County, Lower Jay, *House* 10283, 11 July 1924 (GH)). White bar = 100  $\mu$ m.

*Draba* sp. One fruit, badly preserved and containing no seeds (small, black ascocarps visible on capsule surface), but agreeing in size and shape with several northeastern North American species of this genus. Nineteen native species of *Draba* are listed by Fernald (1950) for the *Gray's Manual* area, eleven species are credited to the Gaspé Peninsula, Quebec (Scoggan, 1950), and eight are given by Polunin (1940) for the Canadian eastern Arctic. The genus is especially rich in calcicoles. FIGURE 42.

*Saxifraga aizoides* L. One seed, spines visible, but cell walls of testa obscured by sediment particles. Seeds of northeastern North American *Saxifraga* species, excluding the rarely fruiting *S. cernua* L. and the geographically isolated *S. gaspensis* Fern. and *S. Geum* L. (which were not studied), have variously ornamented testas (see APPENDIX B). However, only in fully mature seeds of *S. aizoides* do cells of the testa extend outward as long, sharply defined spines. In seed shape and spine arrangement the fossil seed agrees closely with modern reference specimens, and the only difference would seem to be a greater number of spines in the fossil. In North America *S. aizoides* ranges from southern Greenland to Newfoundland, and west to Yukon and eastern British Columbia; it is principally a plant of subarctic and arctic latitudes (although absent from much of the Canadian Arctic Archipelago). In the East *S. aizoides* occurs





FIGURES 38–41. Scanning electron micrographs, seeds of *Silene acaulis* var. *exscapa*: 38, fossil seed from Columbia Bridge site, distorted area at lower left is where radicle breaks through seed coat at germination (see FIGURE 40); 39, seed from herbarium specimen (Canada, Québec, Wakeham Bay, Hudson Strait, *Malte* 126956, 24 July 1933 (GH)); 40, seed recovered from soil adhering to specimen, note ruptured seed coat and fungal hyphae (same collection as in Figure 39); 41, seed from herbarium specimen, possibly less mature than that in FIGURE 39 (Canada, Newfoundland, Bay of Islands region, *Fernald & Wiegand* 3398, 24 July 1910 (GH)). White bar = 100  $\mu$ m.

southward at a few widely scattered places in New England to eastern and western New York. These outlying stations are mostly faces and ledges of wet, calcareous cliffs. FIGURES 26, 82–85.

**Parnassia** cf. **Kotzebuei** Cham. Two seeds, part of the loose, cellular seed coat broken away. In eastern North America, excluding two species of *Parnassia* that extend north only to Virginia, four species are northern (boreal forest or subarctic) in distribution. Seeds of one of these, *P. parviflora* DC., have less distinctly reticulate seed coats and are smaller than seeds of the other species. Seeds of *P. glauca* Raf. and *P. palustris* var. *neogaea* Fern. are the same size as those of *P. Kotzebuei*, but the cellular testa is less pronounced and shiny. We consider the identification of the fossils probable, but not positive, because cells of the testa may have been modified during fossilization. *Parnassia Kotzebuei* exhibits an interrupted range across northern continental North America (southern and western Greenland, northwestern Newfoundland, Gaspé, northern Quebec, Labrador, and from the northwest coast of Hudson Bay to Alaska). FIGURE 27.

**Sibbaldia procumbens** L. Two achenes, which differ from those of *Potentilla* in having apices central and obtusely rounded (cf. FIGURES 28,



29). An arctic-alpine species of disjunct distribution in North America; in the East occurring from southern Greenland to Hudson Bay (and at scattered stations to the west) and southward in the mountains of northwestern Newfoundland, Gaspé, and New Hampshire; in the West from Alaska to California, Utah, and Colorado. FIGURE 28.

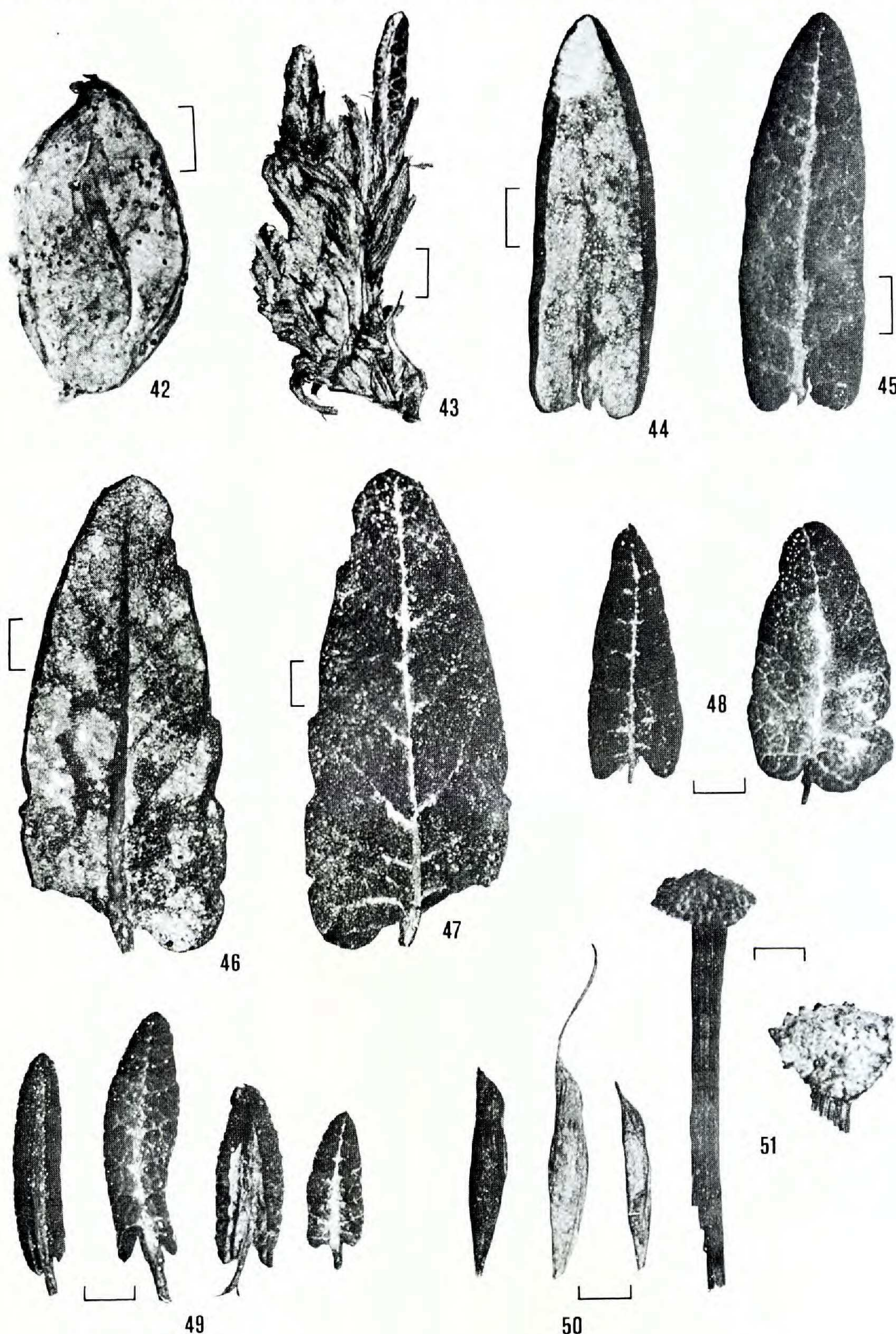
**Potentilla** spp. Seven achenes of different size classes, possibly representing three species; all specimens have smooth walls. The fossils compare favorably in size and shape with achenes of the following northern species of diverse habitats: *P. gracilis* Douglas, *P. hyparctica* Malte, *P. nivea* L., *P. pulchella* R. Br., *P. Robbinsiana* Oakes (endemic to White Mountains, New Hampshire), *P. rubricaulis* Lehm., and *P. usticapensis* Fern. See also APPENDIX B. FIGURE 29.

**Dryas integrifolia** M. Vahl. Numerous isolated leaves and a few leafy plant apices. The fossil leaves are variable in size (3 mm.–1 cm. long) and shape, with margins revolute, entire or sometimes crenulate-dentate. Hollick (1931) identified questioned leaf material of *Kalmia polifolia* Wangenh., *Loiseleuria procumbens* (L.) Desv., and *Vaccinium macrocarpon* Aiton from the Columbia Bridge beds. Study of Hollick's illustrations, in addition to our examination of newly collected limonitic fossils similar to those illustrated by him, suggests that specimens so designated are actually *Dryas integrifolia*. Fossil leaves of *D. integrifolia* are known from several late glacial deposits in Minnesota and at places eastward to Massachusetts (Miller & Benninghoff, 1969), as well as from older late Wisconsinan deposits in this same general region. The species is widespread in arctic North America, where it is a pioneer on raw soil along rivers, cliffs and talus, and beach ridges, particularly on calcareous soils or rock. In eastern North America it occurs southward sporadically to western Newfoundland, Gaspé and Lake Mistassini, Quebec, and southeastern New Brunswick (see map in Miller & Benninghoff, 1969). FIGURES 43–49.

**Dryas Drummondii** Richardson. Abundant leaves; leaf material of this and the preceding species are the most abundant recognizable plant fossils in the deposit. The leaves vary in shape from elliptic to obovate, with bases cuneate in most (a diagnostic character, according to Porsild, 1947) and margins dentate to the apex. A few of the fossil leaves are white-tomentose beneath. Fossils in FIGURES 52–60 were selected to illustrate variation, but leaves of such diverse form can nevertheless be found on herbarium specimens consisting of one or a few plants. *Dryas Drummondii* exhibits an interrupted western–eastern North American distribution (in the East known only from southwestern Newfoundland, Anticosti Island, and the Gaspé Peninsula), with isolated stations along the north shore of Lake Superior (FIGURE 70). It is a plant of calcareous cliffs, talus, and river gravels. FIGURES 52–60.

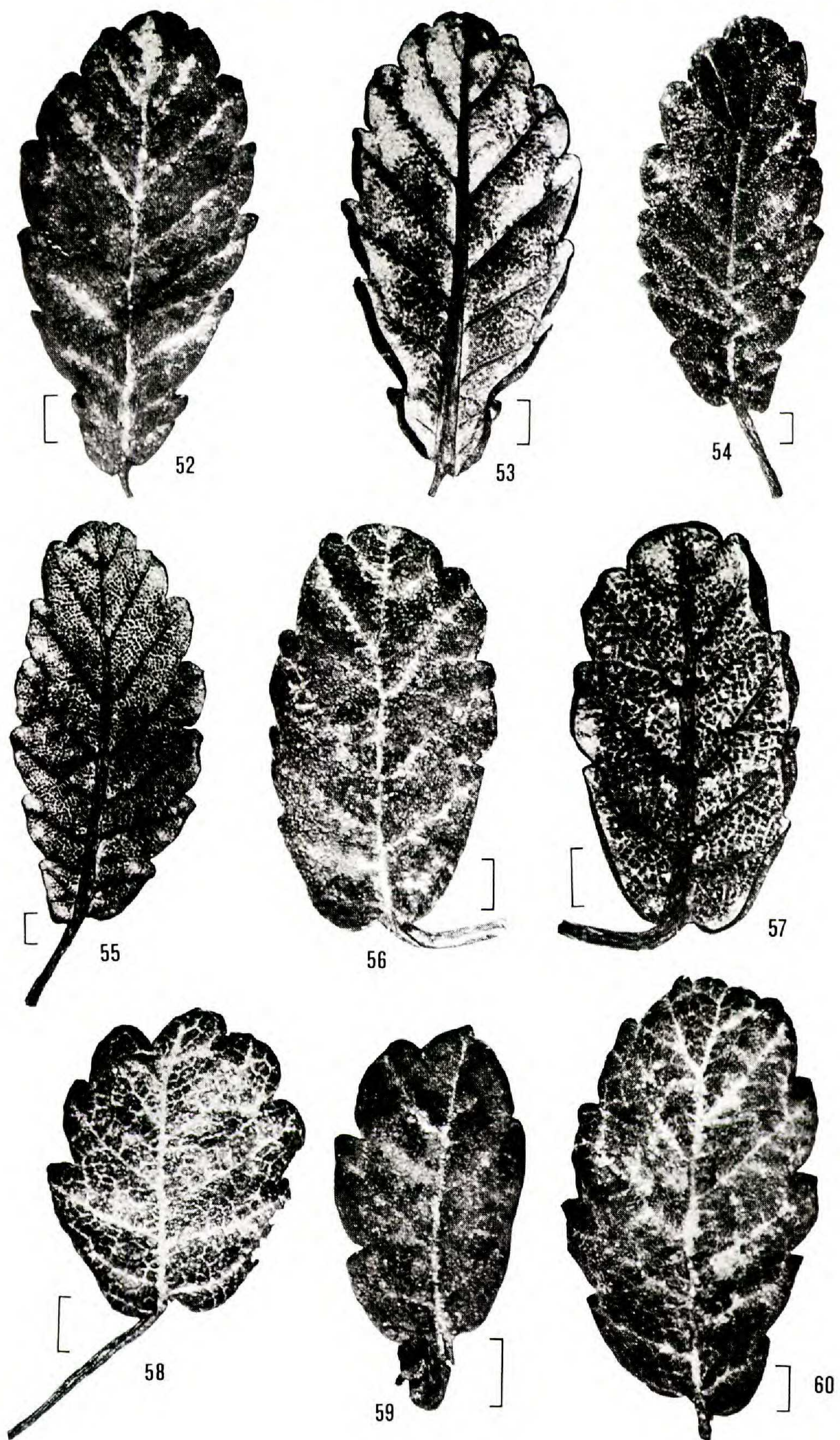
Achenes (plumose styles absent) and receptacles with part of the scape attached were also found. It appears impossible to assign such material to either of the two species. FIGURES 50, 51.





FIGURES 42-51. Plant macrofossils from Columbia Bridge site. 42, *Draba* sp.: capsule. 43-49, *Dryas integrifolia*: 43, portion of plant with two leaves; 44, leaf, lower surface; 45, same leaf, upper surface; 46, leaf, lower surface; 47, same leaf, upper surface; 48, two leaves, upper surfaces; 49, four leaves, (from left) lower, upper, lower, and upper surfaces. 50, *Dryas* sp.: three achenes. 51, *Dryas* sp.: two receptacles, scapes partly preserved. Scale lines = 1 mm.





FIGURES 52-60. Plant macrofossils from Columbia Bridge site. *Dryas Drummondii*: 52, leaf, upper surface; 53, same leaf, lower surface; 54, leaf, upper surface; 55, same leaf, lower surface; 56, leaf, upper surface; 57, same leaf, lower surface; 58-60, three other leaves, upper surfaces. Scale lines = 1 mm.



**Geum** sp. Two receptacles, achenes immature, styles recurved, petals absent, calyx weakly campanulate; further identification not possible because of incomplete preservation. Fernald (1950) lists eight native species for temperate eastern North America. They are plants of dry to moist mineral soils, sometimes wet peats, usually in sparse woods or thickets. *Geum macrophyllum* Willd. and *G. rivale* L. extend northward to southern Labrador.

**Elaeagnus commutata** Bernh. ex Rydb. One ellipsoid body representing the hardened and eight-ridged inner wall of the calyx tube; four immature fruits with the calyx tube more or less enlarged and fleshy and a portion of the perianth and style persisting, peltate scales visible as punctae. A shrub of dry calcareous slopes, *E. commutata* exhibits an interrupted transcontinental range (FIGURE 70), with eastern stations limited to the Gaspé Peninsula and westward along the St. Lawrence River valley; the western segment of its range extends from the James Bay region to central Alaska, south to northern Utah. FIGURES 61–63.

**Shepherdia canadensis** (L.) Nutt. Two seeds, one staminate flower, and four twigs with opposite leaf scars or terminal, appressed, paired leaves; peltate scales visible on leaves and twigs. Well-preserved seeds are black and shiny and have a short point near the apex, a notch to one side near the base, and a shallow, inconspicuous groove in between. Like the preceding species, *S. canadensis* is a shrub of calcareous mineral soils and open habitats (e.g., slopes, sandy shores, sparse spruce woodlands). It is distributed from Newfoundland to Alaska, and, in the East, south to Nova Scotia, central Maine, Vermont, and western New York. On the basis of fossil pollen, Richard (1974) established that *S. canadensis* was more widely distributed in Quebec during late glacial and early postglacial times than it is now. FIGURES 30, 64.

**Ledum groenlandicum** Oeder. Nine leaves, the margins revolute and brown-tomentose beneath; two capsules, one with four valves, the other with five, dehiscent from the base. *Ledum groenlandicum*, a common low shrub of boreal North America, occurs from southern Greenland to Alaska, and, in the East, southward (and often discontinuously in isolated peat bogs) to northern New Jersey, Pennsylvania, and Ohio. FIGURES 65–67.

**Arctostaphylos Uva-ursi** (L.) Sprengel. Eleven fruit stones or fruit stone halves, in one case two fruit stones fused together laterally. Fruits from a selection of herbarium specimens show that stones can be free or fused to form a partial or complete ring. Compressed laterally, the individual stones are wedge shaped in cross section and have a gap in the wall near the base of the dorsal suture. Represented by var. *coactilis* Fern. & Macbr. in the southern part of its range, *A. Uva-ursi* occurs from Newfoundland and Labrador to Alaska, south to Long Island, Virginia, western New York, and northern Illinois, on well-drained soils or on rocks.

**Vaccinium uliginosum** var. *alpinum* Bigelow. Numerous obovate or elliptic leaves, generally 1 cm. or less long, reticulate venation visible in



some; one seed, similar to those of *V. uliginosum* in size and shape and in having the testa comprised of linear cells with thin anticlinal walls. Seeds of *Vaccinium* are more or less elliptic in side view but with one long side convex and the other straight or concave. Seeds differ in size (although within one fruit, smaller, possibly aborted, seeds are present) and in shape (e.g., round to triangular in cross section). Cells of the seed coat may be long (most species of northeastern North America) or short (*V. angustifolium* Aiton, *V. vacillans* Torrey). Anticlinal walls of the testa may be thick (*V. Oxycoccus* L., *V. vacillans* Torrey) or thin. When wet, the thin, transparent outer periclinal wall bulges outward, but when dry the testa is reticulate or areolate. In the southeastern part of its range (northern New York and New England), *V. uliginosum* var. *alpinum* occurs mostly on summits of the higher mountains. Otherwise, it occurs widely throughout boreal America from Newfoundland to Alaska. FIGURE 68.

**Compositae.** Two achenes, of identical size and shape, a few pappus bristles present at the apex of one. We have not been able to identify the fossils more precisely, but their occurrence establishes the presence of reproducing plants of this predominantly herbaceous family. FIGURE 31.

**Musci.** Intermixed with macrofossils of vascular plants were well-preserved but small (generally less than 0.5 cm. long) leafy fragments of mosses. Although fossil Musci compose a minor part of the sieve residues, 32 species representing extant mosses have been identified. These form the basis of a separate study (Miller, unpubl. ms.) and are only briefly discussed here.

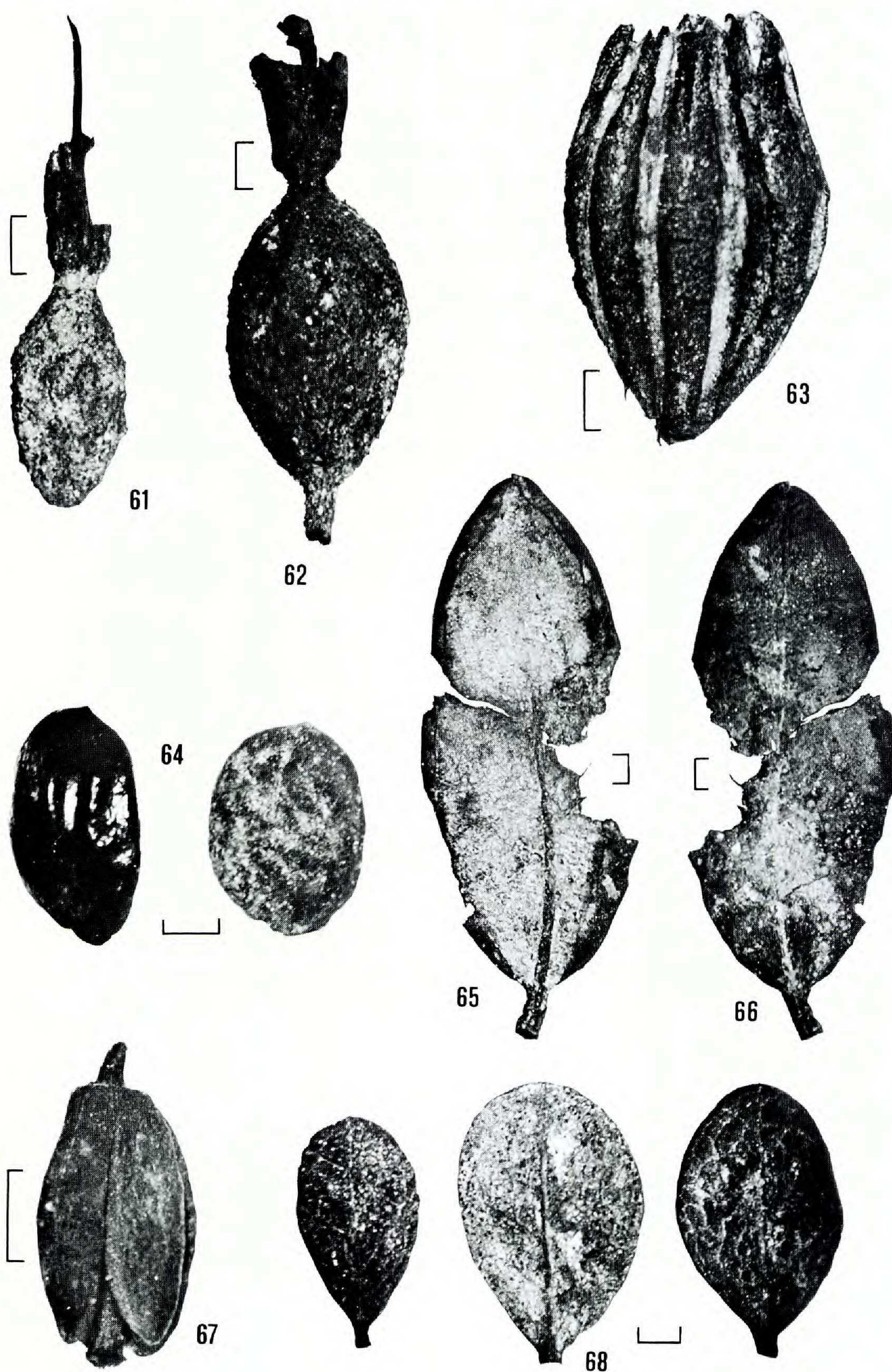
The moss assemblage contains no strictly arctic or subarctic species. Mosses now mostly northern in distribution are represented, however, and some occur well into the arctic zone. Only one, *Hygroamblystegium tenax* (Hedwig) Jenn., which in eastern North America ranges from Florida and Arkansas northward to southern Canada, could be termed a southern species. Other members of the assemblage, for example *Catoscopium nigrum* (Hedwig) Bridel, *Cratoneuron commutatum* var. *falcatum* (Bridel) Moenk., and *Scorpidium turgescens* (T. Jensen) Loeske, are widespread in the North but sporadic and local along the southern edge of their ranges, which may extend to the northern United States. Species with present-day disjunct eastern-western North American distributions are represented (e.g., *Timmia austriaca* Hedwig, *Tortella inclinata* (R. Hedwig) Limpr., and *Hypnum revolutum* (Mitten) Lindb., although the range of the last in North America has not been fully documented).

The assemblage consists almost entirely of species found in calcareous habitats. These include hygric phases of rich fens (*Drepanocladus revolvens* (Sw.) Warnst., *D. vernicosus* (Lindb. ex C. Hartman) Warnst.,

---

FIGURES 61–68. Plant macrofossils from Columbia Bridge site. 61–63, *Elaeagnus commutata*: 61, 62, immature fruits, peltate scales visible as punctae; 63, ellipsoid, eight-ridged inner wall of calyx tube surrounding seed (from mature





fruit). 64, *Shepherdia canadensis*: two seeds. 65–67, *Ledum groenlandicum*: 65, leaf, lower surface; 66, same leaf, upper surface; 67, capsule. 68, *Vaccinium uliginosum* var. *alpinum*: three leaves, (from left) upper, lower, and upper surfaces. Scale lines = 1 mm.



and *Scorpidium turgescens* (T. Jensen) Loeske), calcareous seeps or streams (*Hygrohypnum luridum* (Hedwig) Jenn.), and moist to dry calcareous rocks or soil (*Ditrichum flexicaule* (Schwaegr.) Hampe, *Dicranella varia* (Hedwig) Schimper, *Hypnum vaucheri* Lesq.). While a few of the species represented can occur beneath forest cover, no characteristic forest species are present. Thus, the assemblage indicates the presence of several distinct wet to dry, nonforest communities rich in calcicolous species.

## INTERPRETATION

### RADIOCARBON AGE DETERMINATIONS

The age of the laminated sediments has been established by radiocarbon dating. Two of the dates were from wood fragments picked from the sediment. The upper, at 0.84 meter below the top of the deposit, is  $11,390 \pm 115$  years B.P. ( $\delta^{13}\text{C} = -27.5$  ‰; WIS-919). The lower, at 1.52–1.58 meters, is  $11,540 \pm 110$  years B.P. ( $\delta^{13}\text{C} = -29.0$  ‰; WIS-961). However, a block of sediment rich in organic matter from an intermediate depth, 1.36–1.45 meters, yielded an age of  $20,500 \pm 250$  years B.P. (WIS-925). We reject this last date. The sediment submitted for dating was calcareous clay, silt, and sand containing abundant *Potamogeton* leaves, in addition to other plant remains. Donner *et al.* (1971) demonstrated that living plants of *Potamogeton* can give radiocarbon ages up to 3000 years old. During photosynthesis, aquatic plants can utilize carbon dioxide and carbonate and bicarbonate ions in solution that may contain carbon derived from ancient sediments. We conclude that this effect may be in part responsible for an age determination that is too old in relation to the other dates and to its stratigraphic position. However, the difference between the older and younger age determinations is greater than that attributable to the effect of “old” carbon. In view of the sedimentary setting of the deposit and the stratigraphic relation of the dated levels, we think that rebedded interstadial organic material is an unlikely cause. With the new ion counting technique of radiocarbon dating (see Stuiver, 1978), it may be possible to date associated wood fragments and leaves separately, and thereby to determine if they are of different age.

The radiocarbon ages reported here are the first to be determined directly for any lacustrine sediment in the Connecticut River valley. Consequently, they are important for a better understanding of the glacial history of New England. If the Columbia Bridge sediments are glaciolacustrine, these radiocarbon dates demonstrate that 11,500 years ago there was an ice margin in the upper Connecticut River valley drainage near the site. In Quebec, by 11,500 years ago an active ice margin had retreated to the St. Lawrence Lowland (Gadd *et al.*, 1972), and the Champlain Sea had been in existence for over 500 years (Cronin, 1977; Occhietti & Hillaire-Marcel, 1977). Thus, an ice margin in the upper Connecticut drainage at this same time would represent a local glacier, perhaps an active ice cap



or a long-lived stagnant mass of ice. Several workers (Flint, 1951, 1953; Schafer, 1968; Prest, 1969; Shilts, 1976) have proposed the existence of late glacial ice caps in the White Mountains and in other areas of northern New England. In the Thetford Mines area of Quebec, LaMarche (1971) reported evidence for late Wisconsinan north-flowing ice. Shilts (1976) concluded that ice flowed north and northwest from an ice mass stranded in the area of the international boundary in Maine and Quebec. In northwestern Maine, 128 km. northeast of Columbia Bridge, Hanson and Caldwell (1977) found end moraines and glacial striae that indicate ice flow southeastward from an ice cap stranded on the Boundary Mountains. They tentatively date these moraines at 11,000–12,000 years B.P., a time that postdates the marine invasion of the St. Lawrence Valley.

We conclude that the 11,500-year-old sediments at Columbia Bridge are glaciolacustrine. Their deformation indicates that they may have been deposited on or adjacent to a mass of stagnant ice. With the evidence at hand, we can not determine the character of the lake's dam, and we are uncertain at which end the valley was dammed. However, the presence of a glacial lake in the Upper Connecticut Valley between 11,000 and 12,000 years ago supports the hypothesis of a local glacier in northern New England and southern Quebec at that time.

#### VEGETATION

Several lines of evidence are available for a reconstruction of vegetation and environments near the fossil site 11,500 years ago. Chief among these are the pollen spectra and plant macrofossils. Animal fossils in the deposit, which include molluscs, ostracods, and insects, are currently under study by various specialists, and paleoecological data from this work will supplement conclusions reached from an analysis of the plant remains.

#### Pollen Analyses

GENERAL. Before a botanical interpretation of the pollen assemblages is presented, two important influences that have modified the spectra will be discussed: 1) weathering, which is restricted to the upper part of the laminated sediment, and 2) the constant presence of deteriorated pollen and spores.

Evidence of oxidation in the laminated sediments above 0.75 meter has already been described. Oxidative degradation of the microfossils during weathering is the likely cause of differences between spectra near the top and bottom of the profile. Different kinds of pollen resist oxidation in varying degrees (Sangster & Dale, 1964). Among pollen or spore types represented in the sediments (FIGURE 2), *Pinus*, *Quercus*, *Carpinus-Ostrya*, Polypodiaceae, and Lycopodiaceae appear to have been the most resistant to *in situ* weathering; *Picea*, *Juniperus-Thuja*, *Corylus*, and Cyperaceae were less resistant; and *Abies* seems mostly to have been eliminated from



the weathered zone. Those types relatively unaffected by oxidation were *Fraxinus*, *Betula*, *Artemisia*, and high-spine Compositae.

The relatively constant proportion of deteriorated and unknown pollen and spores in sediments below 0.75 meter indicates continuous input of deteriorated grains. Most of these were degraded (*sensu* Cushing (1964)) since they had an abraded appearance or unresolvable exine stratification. Degraded pollen in late glacial lake sediments is generally interpreted as originating from till through redeposition (Cushing, 1964), but confirmation of this process may be difficult to obtain. Also, sediments of large lakes (according to Lougee (1939), Lake Colebrook was perhaps 35 km. long and up to 2 km. wide) have been found to contain a higher proportion of deteriorated and unknown grains than do sediments of small lakes (McAndrews & Power, 1973). This may be because larger lakes often have extensive watersheds, and pollen deposited in them spends time exposed to air on surrounding surfaces before being washed into the basin. Cushing (1964) called such pollen "penecontemporaneous" to distinguish it from pollen reaching a basin directly by air. Exines of pollen in and on soil are often distinctively corroded by microbial activity.

While it is not possible to determine accurately the size of the watershed that fed Lake Colebrook, to judge from deltaic deposits exposed in 1977 along the west side of the valley near the fossil site, it appears that tributary streams entered the lake. The lenses of organic detritus also indicate periodic input of terrestrial plant matter, perhaps by stream action. It is surprising, therefore, that no pollen showing evidence of microbial corrosion was observed during our counts. The reason for the absence of this type of deteriorated pollen is not known. Studies of even small lakes with tributaries (Peck, 1973) have shown that 90–96 percent of the pollen can be stream carried. Most stream-borne pollen presumably comes from nearby upland surfaces that contribute pollen accumulated in soils or other traps and by erosion of fossiliferous sediments and rocks. Although we cannot demonstrate a probable source, most of the deteriorated pollen and spores may possibly have been redeposited from till. Unfortunately, degraded and corroded grains are not always distinct microscopically, and the process of deterioration of pollen and spores on recently deglaciated surfaces has been poorly investigated.

The age of the degraded microfossils is unknown, but interstadial, interglacial, or even Tertiary deposits are possibilities. Among the unknown pollen grains in the sediments were some that resembled *Engelhardtia*, which is present in the early Tertiary Brandon lignite of west-central Vermont (Traverse, 1955). Grains resembling *Platycarya*, common in the Tertiary elsewhere, are also present. Late glacial inorganic lake sediment often contains these and other redeposited Tertiary microfossils (Iversen, 1936; M. Davis, 1961; Cushing, 1964, 1967), especially in areas of Tertiary bedrock. However, *Engelhardtia*- and *Platycarya*-like grains from the Columbia Bridge deposit cannot be positively identified because of poor preservation. These Tertiary pollen types are flattened, while most pollen and spores in our samples were inflated. Therefore, in the absence of any



definite and abundant Tertiary pollen types, we think that the redeposited microfossils are mostly from Pleistocene plants and are rebedded from Pleistocene sediments.

Percentages of various pollen types below 0.75 meter are relatively consistent from spectrum to spectrum, and these pollen assemblages form the basis of the vegetational interpretation discussed below. The assemblages could have been modified arithmetically by subtracting all deteriorated pollen from the totals, but this was not done because the percentage of deteriorated pollen is also more or less constant throughout the unweathered interval.

**POLLEN SPECTRA BELOW 0.75 METER.** Although there is evidence of rebedded pollen in the profile, spectra below 0.75 meter are nevertheless similar to assemblages from basal small lake and bog sediments at sites in northern New England and adjacent Quebec. Remarkably similar is the lower part of zone A at Brownington Pond, Vermont (M. Davis, 1965), 47 km. west of Columbia Bridge. At both sites pollen of *Picea* and *Pinus* are the most frequent types (ca. 40–50 percent), and *Juniperus-Thuja* and *Quercus* are the next most prominent. *Betula* percentages are low (5 percent or less). Pollen of herbs (mostly Cyperaceae) and shrubs total 30 percent. Spectra from zone 8 at Barnston Lake, Quebec (Mott, 1977), which is 37 km. northwest of Columbia Bridge, are also similar except for higher *Betula* and lower Cyperaceae percentages.

The radiocarbon age of the Brownington Pond sediments has not been reported, but the Barnston Lake spectra are dated at slightly older than 11,150 years B.P. Radiocarbon dates of  $11,030 \pm 200$  and  $11,290 \pm 200$  years B.P. have been reported for basal sediments of Bugbee Bog, Caledonia County, Vermont, 72 km. southwest of Columbia Bridge (McDowell *et al.*, 1971). The radiocarbon-dated interval at this site was not analyzed for pollen, but spectra from levels just above the dated interval in an adjacent core are dominated by pollen of *Picea* and *Pinus* with some *Betula* and *Salix* ( $\Sigma$  = total AP); percentages of Cyperaceae and other herbs are less than 1 percent ( $\Sigma$  = AP + NAP + spores). These spectra differ greatly from the Columbia Bridge assemblages. Whitehead and Bentley's profile (1963) from Pownal Bog in southwestern Vermont includes only a basal zone dominated by *Picea* with some *Pinus* and *Abies* but lacking an appreciable amount of herb or shrub pollen.

The detailed pollen diagram of R. Davis *et al.* (1975) from Moulton Pond in southern coastal Maine, 225 km. east of Columbia Bridge, includes a lengthy radiocarbon-dated interval that is in part contemporaneous with deposition of the Columbia Bridge laminated sediments. Spectra of similar age from the two localities correspond fairly closely. The principal differences include somewhat larger percentages of *Betula*, *Alnus*, and Gramineae, the presence of *Myrica*, and the absence of *Juniperus-Thuja* at Moulton Pond.

R. Davis *et al.* (1975) review the evidence that such pollen assemblages represent tundra vegetation. This includes similarity between percentage



composition of surface pollen accumulations in present-day areas of tundra and fossil spectra and also corresponding pollen influx values, i.e., a similar number of grains deposited/cm.<sup>2</sup>/year.

Pollen assemblages with large relative amounts of Cyperaceae pollen (ca. 20 percent) in association with *Picea* (ca. 30 percent), *Pinus* (ca. 15 percent), and lesser percentages of *Betula*, *Alnus*, *Salix*, and Gramineae are being deposited today in the tundra and tundra-forest ecotone of northern Quebec and Labrador (R. Davis & Webb, 1975). Columbia Bridge spectra differ somewhat from the current pollen rain of that region in having slightly less *Alnus* and *Betula*, as well as in including *Quercus* and other Temperate Zone deciduous trees. In eastern North America the consistent occurrence in late glacial sediments of pollen of *Quercus*, *Acer*, *Carya*, *Carpinus* and/or *Ostrya*, and other thermophilic trees is a well-known but puzzling phenomenon. That trees of these genera were in fact established on the late glacial landscape has not been demonstrated by macrofossil finds. This pollen may thus either represent rebedded contaminants or have been carried by air from a distant source. Even though present in low concentration, such wind-blown pollen becomes prominent in percentage data if the parent vegetation is characterized by low pollen influx. At Moulton Pond influx values during the presumed tundra phase varied from 150 to 920 grains/cm.<sup>2</sup>/yr. This is well within the range of influx reported by Ritchie and Lichti-Federovich (1967) for tundra sites in arctic North America and is also among values calculated by R. Davis and Webb (1975) for other New World tundra localities.

If it is assumed that the Columbia Bridge rhythmites are varves, pollen influx at the site 11,500 years ago was 4600 to 6600 grains/cm.<sup>2</sup>/yr. (TABLE 2). Tributary-fed Lake Colebrook perhaps accumulated sediment with a low airborne component, as do comparable modern small lakes that contain 4–10 percent pollen deposited out of air (Peck, 1973). If true, this reduces influx to 184 to 660 grains/cm.<sup>2</sup>/yr. Influx determinations of pollen deposited in open Petri dishes at tundra localities in the New World Arctic (Ritchie & Lichti-Federovich, 1967) vary from 5 to 762 grains/

TABLE 2. Pollen and spore concentration and influx.

DEPTH (m.)	POLLEN AND SPORE CONCENTRATION (number/cc.)	RHYTHMITE THICKNESS (cm.)	INFLUX (number/cm. <sup>2</sup> /yr.)
0.0–0.05	67	1.20	81
0.20–0.25	165	2.04	336
0.50–0.55	889	1.56	1387
0.80–0.85	1470	3.24	4765
1.10–1.15	2774	2.38	6603
1.35–1.40	3322	1.73	5747
1.55–1.60	2174	2.13	4631



cm.<sup>2</sup>/yr. ( $\bar{X}$  = 200). Influx values of from 2000 to 3000 grains/cm.<sup>2</sup>/yr. are also within the range of values reported for tundra localities by other workers (M. Davis *et al.*, 1973) or correspond to measurements taken in the boreal forest-tundra ecotone (R. Davis *et al.*, 1975, *t.* 1), where trees are sparsely represented. Thus, both pollen percentages and pollen influx data from the Columbia Bridge deposit indicate that the landscape was essentially treeless in the area of the site 11,500 radiocarbon years ago.

Apart from Moulton Pond, evidence of late glacial tundra in sediments at other sites near the Columbia Bridge deposit has been reported by Mott (1977) and Richard (1977). Zone 8 at Barnston Lake was interpreted by Mott (1977) as representing tundra, which at this locality was replaced by taiga 11,200 years B.P. Following a detailed regional study of sites north and south of the St. Lawrence River, Richard (1977) recognized a tundra phase that existed from 11,500 to 11,000 years B.P. at localities close to northern New England. Palynological evidence of tundra is present in Richard's Mont Shefford and Albion profiles (Richard, 1977), which are 105 km. northwest and 118 km. north of Columbia Bridge, respectively. Arboreal pollen types at these two sites range between 40 and 70 percent during the tundra phase, but pollen concentration values are high (ca. 10,000 to 75,000 grains/cc.). Influx determinations are not available for the sites.

In older sediments at Mont Shefford and Albion, pollen concentration values are much lower and approach those recorded at Columbia Bridge. Richard (1977) has interpreted these older sediments as containing a record of "periglacial desert" in which herbs and lichens occurred sparsely on the landscape prior to development of a more continuous cover of vegetation during the succeeding tundra phase.

### Macrofossils

The occurrence of plant macrofossils at Columbia Bridge permits an evaluation of the periglacial desert hypothesis and also of the more general interpretation that low pollen influx and high herb and shrub to tree pollen ratios indicate a treeless, tundra-type vegetation. The abundance and diversity of plants recovered as macrofossils indicate the presence of a rich flora comprised of species that presently grow in a variety of habitats. Most of the species are herbs or low-growing shrubs. The landscape appears to have supported relatively few trees, and these were spruce (*Picea* sp.) and balsam poplar (*Populus balsamifera*). It is not possible to decide whether these occupied positions on exposed upland slopes or in sheltered places along streams and valleys in the adjacent upland. Balsam poplar is a fast-growing tree that pioneers in disturbed areas along streams and rivers in the present-day boreal forest. Species of spruce are also common colonizers of recently disturbed mineral soils.

The macrofossils also permit more precise identification of species in the flora than otherwise would be possible from pollen alone. Pollen of *Juniperus* and *Thuja* (Cupressineae of many pollen analysts) is so similar



as to be essentially indistinguishable in the fossil condition. At Columbia Bridge *Juniperus-Thuja* pollen is most certainly of *Juniperus communis* because abundant macrofossils of this species, including a microsporangiate strobilus, occur in the deposit. The status of *Populus* in late glacial sediments is uncertain because its pollen may be difficult to identify and, in fact, is not always preserved. Mott (1978) has recently redrawn attention to these problems and, with new data, concluded that *Populus* perhaps had a significant role during the change from tundra to forest. For eastern North American sites some workers indicate that *P. cf. tremuloides* (Richard, 1977; identification based on pollen) was the species involved; others suggest *P. balsamifera* (M. Davis, 1958; identification based on pollen). At Columbia Bridge the poplar present was *P. balsamifera*. Macrofossils of the various identified species of *Carex* and *Salix* and of *Betula* similarly help to define the late glacial flora. However, determination of how widespread the identified species in these genera may have been 11,500 years ago must await discovery of macrofossils at additional sites.

Apart from the pondweeds, *Potamogeton filiformis* and *P. pusillus*, which grew submerged, probably along the shore of Lake Colebrook or in shallow ponds drained by waters flowing into the lake, no other aquatic seed plants are represented in the macrofossil assemblage. However, *Carex aquatilis* is a plant of wet habitats. *Selaginella selaginoides*, *Ranunculus Cymbalaria*, and a few other species grow on moist soil among rocks near running or stationary water. Remaining members of the vascular plant assemblage are plants of better-drained sites, and these species may form a fair sample of the flora that grew on upland, nonaquatic surfaces. The moss assemblage can similarly be divided into a species group typical of wet habitats and another of drier sites. Aquatic and semiaquatic species are best represented in the moss assemblage, indicating that the landscape near the fossil site was provided with a variety of wet habitats such as rich fens, fen margins, seeps, and streamsides. Drier sites interspersed among these, including ridgetops and slopes, upland bedrock areas, gravel bars along tributary streams, and beach deposits, are indicated by non-aquatic members of both moss and vascular plant macrofossil assemblages.

The lack of soil maturity or the presence of periodically disturbed sites is indicated by the abundant occurrence in the deposit of *Dryas Drummondii*, which is a pioneer on calcareous river-gravels, talus slopes, and bluffs. At the present time in lowland areas along rivers of the Gaspé Peninsula, this species and balsam poplar are conspicuous associates. *Dryas integrifolia*, *Saxifraga aizoides*, *Sibbaldia procumbens*, and other seed plants in the assemblage can also pioneer in suitable habitats. In certain currently glaciated areas, for example at the terminus of the Athabasca Glacier in Alberta, *Dryas Drummondii* and *Saxifraga aizoides* are among the first conspicuous angiosperms to become established on the moraines.

Species represented in the macrofossil assemblages are of ecological interest from two other standpoints. Nearly all are calcicoles. Among the identified seed plants for which such information exists, only *Betula glandulosa*, *B. pumila*, *Silene acaulis* var. *exscapa*, *Sibbaldia procumbens*, *Ledum groenlandicum*, and *Vaccinium uliginosum* var. *alpinum* show current pref-



erences for acidic substrata. The list of mosses in this category is shorter. The significance of this observation will be discussed further under the heading "phytogeography," but the raw, recently exposed drift and bed-rock surfaces near the fossil site must have been predominantly calcareous. Four members of the macrofossil assemblage, *Dryas integrifolia*, *D. Drummondii*, *Elaeagnus commutata*, and *Shepherdia canadensis*, through the activity of an endophyte in root nodules, have the capacity for nitrogen fixation (Silvester, 1977). A fifth, *Alnus*, may also have been present, although there is only palynological evidence for its occurrence. Nitrogen-fixing plants play an important role in enriching raw glacial soils (Lawrence *et al.*, 1967).

In summary, both pollen and macrofossil data indicate the presence of an essentially nonforested landscape in the Columbia Bridge area 11,500 years ago. Floristic diversity was high. Many kinds of herbs or low woody plants of herbaceous habit were represented, some of which have current arctic-alpine distributions. Thickets of low shrubs (*Betula*, *Salix* spp., *Elaeagnus*, *Shepherdia*) were present, as was some balsam poplar and spruce. A mixture of well- and poorly-drained habitats was available to support the species of mosses and seed plants represented, which have diverse edaphic requirements.

#### PHYTOGEOGRAPHY

The Columbia Bridge fossil plant assemblage consists of species that at the present time are broadly northern in distribution. While some of the plants now occur well into the Subarctic and Arctic, the entire assemblage does not strictly qualify as an arctic one. Nevertheless, certain of the species, including *Salix Uva-ursi*, *Betula glandulosa*, *Oxyria digyna*, *Silene acaulis* var. *exscapa*, *Saxifraga aizoides*, and *Sibbaldia procumbens*, are present members of an arctic-alpine element in the flora of the northeastern United States. These plants are currently of restricted distribution in the New England area. For example, *Oxyria digyna* and *Sibbaldia procumbens* are presently found only on Mt. Washington, New Hampshire, in alpine habitats (Pease, 1964) such as Tuckerman and Huntington ravines and the Great Gulf. *Silene acaulis* var. *exscapa* is similarly restricted to the summit areas of Mt. Washington and Mt. Katahdin, Maine. Of more general alpine distribution are *Salix Uva-ursi* and *Betula glandulosa*, which occur on a number of the higher mountain summits of Vermont, New Hampshire, and Maine. The low elevation occurrence of fossils of these alpine species is consistent with the hypothesis that the alpine flora developed from populations of arctic and subarctic plants that lived at many different elevations during the waning phases of glaciation (see Fernald, 1907). Restriction to mountain summits occurred as the lowlands become climatically and/or edaphically unsuited to continuation of populations at all elevations.

The present-day localization of arctic-alpines in New England and southeastern Canada was first discussed and evaluated in detail in Fernald (1907), who noted that arctic and subarctic disjuncts in this region could



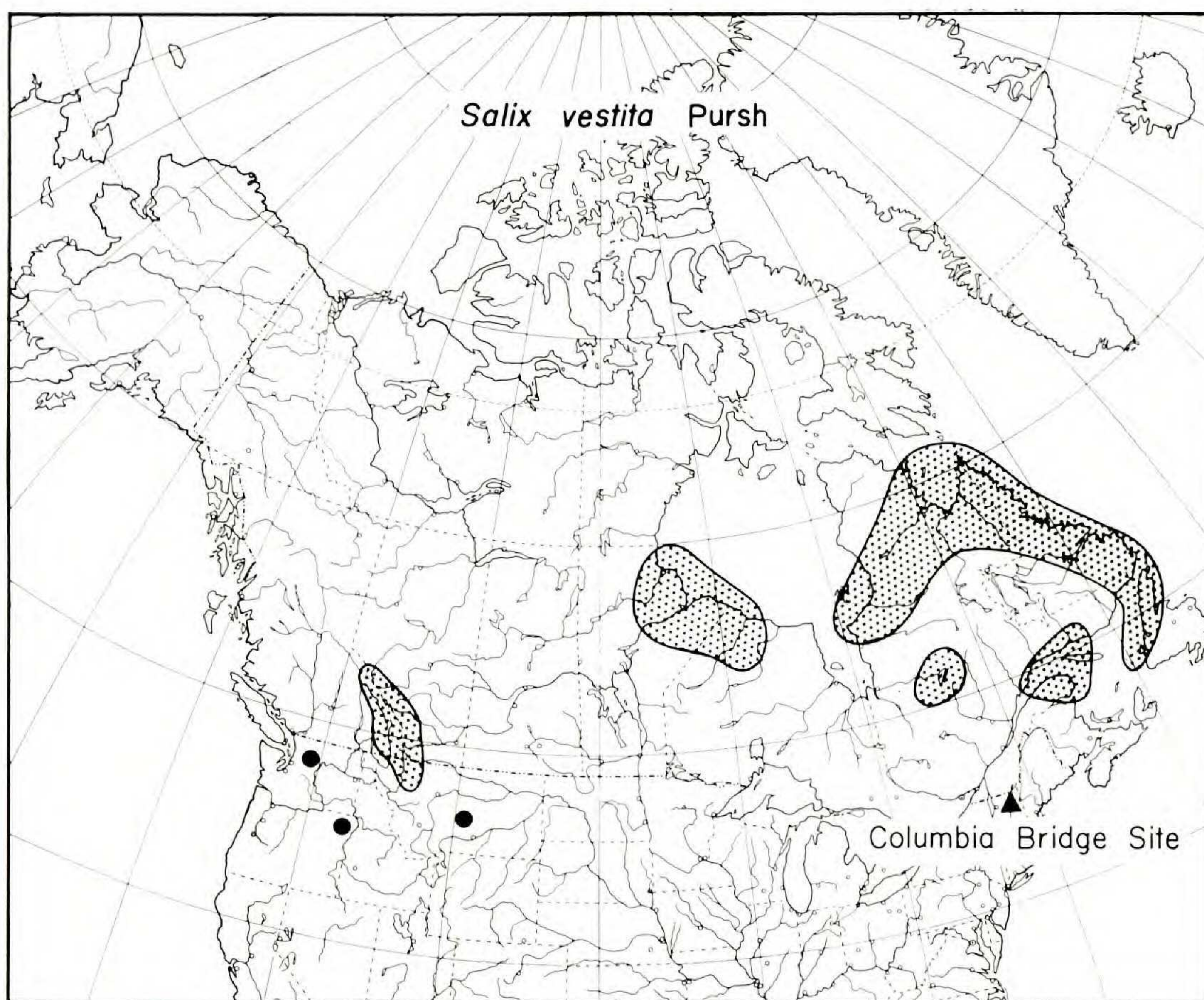


FIGURE 69. North American distribution of *Salix vestita* based on maps in Fernald (1925) and Raup (1943, 1959), specimens in A and GH, and data of Hitchcock and Cronquist (1964). Additional localities in Montana are given by White (1956). Triangle shows location of Columbia Bridge site.

be grouped into three categories that correspond to areas of acidic, calcareous, or serpentine rock. Alpine species of acidic soil preference are mostly restricted to the highest mountain summits (e.g., Mt. Mansfield, Vermont; Mt. Washington and nearby peaks; Mt. Katahdin), the coastal cliffs of eastern Maine, and Mont Jacques Cartier and vicinity on the Gaspé Peninsula, Quebec. Serpentine rock is rare in mountain areas of New England but occurs on the Gaspé (Mont Albert tableland). Localized areas of calcicolous alpine plants do not coincide with the highest elevations in New England, presumably because calcareous bedrock is absent from high alpine areas. Places rich in calcicoles include such low and moderate elevation areas as Smuggler's Notch on the east flank of Mt. Mansfield, the Willoughby Cliffs in northern Vermont, river cliffs of northern Maine and adjacent New Brunswick, sea cliffs along the north and east Gaspé coasts, and river bluffs and mountain spurs of interior Gaspé.

Subsequent floristic work in New England and regions immediately to the north have upheld Fernald's conclusions about the localization of alpine plants. Fossils from the Columbia Bridge deposit are of species that belong to his acidic and calcareous groups; no fossils of species in the shorter list of serpenticolous plants were found. The association of



plants exhibiting different current soil preferences indicates the existence of ecologically diverse mixtures of species during late glacial time. In view of present-day restriction of alpine plants and the prevailing theory that called for northward migration of the boreal flora following ice withdrawal, Fernald (1907) had difficulty accepting that plants with such specific edaphic requirements could have grown together during the time of northward migration. He resolved the dilemma by supposing that raw glacial soils, having been brought together from a variety of sources, presented required nutrients in amounts that permitted heterogeneous mixtures of species to coexist. This hypothesis is attractive, but it ignores the possible role of competition, the lack of which prior to the establishment of forest cover, and on unstable, regularly rejuvenated surfaces, may have allowed unusual species associations to become established, particularly if the plants involved were pioneers. The absence of competition from trees is considered significant in explaining the presence of disjunct plants on soils of high base status in parts of Britain (Pigott & Walters, 1954). The same phenomenon helps to account for the localization of calcicolous plants on calcareous cliffs and ledges in the New England area where they form "islands" surrounded by communities of different composition.

Among the plants represented in the Columbia Bridge deposit the fol-

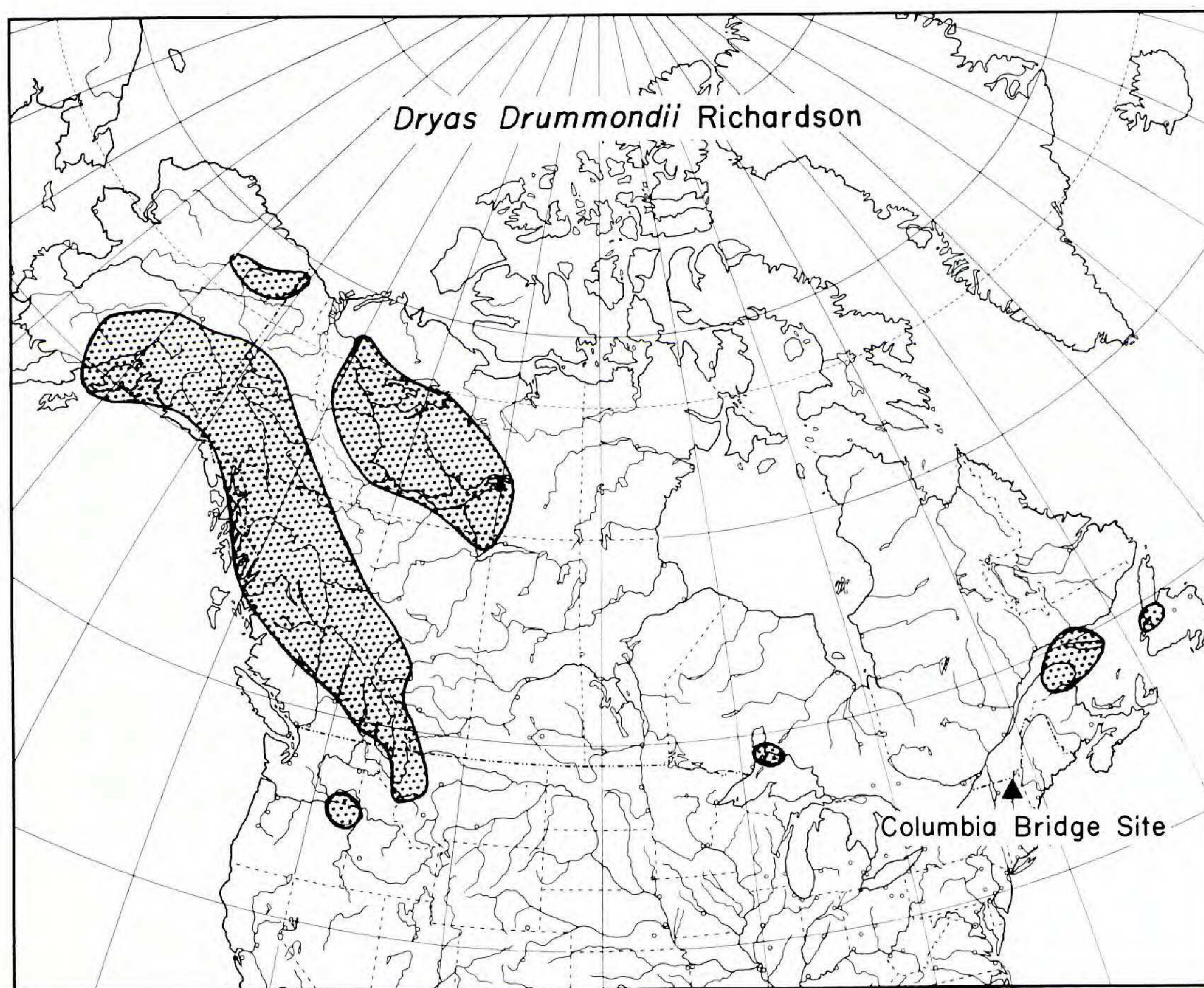


FIGURE 70. North American distribution of *Dryas Drummondii* based on maps in Hultén (1968), Rouleau (1956), and C. Rousseau (1974). Triangle shows location of Columbia Bridge site.



lowing are considered calciphiles (Fernald, 1907): \**Selaginella selaginoides*, \**Juniperus communis* var. *montana*, *Salix vestita*, \**Saxifraga aizoides*, *Parnassia Kotzebuei*, *Dryas integrifolia*, *Dryas Drummondii*, \**Shepherdia canadensis*, and *Elaeagnus commutata*. Only those preceded by an asterisk are members of the present flora of New England, and most of these are known from only a few localities (Seymour, 1969). The following Columbia Bridge plants are species of acidic soils (Fernald, 1907), and all are present members of the New England flora (Seymour, 1969): *Salix Uva-ursi*, *Betula glandulosa*, *Oxyria digyna*, *Silene acaulis* var. *exscapa*, *Sibbaldia procumbens*, *Ledum groenlandicum*, and *Vaccinium uliginosum*. All are strictly alpine except *Ledum*, which also grows at low elevations in acid peatlands.

In addition to species that exhibit arctic-alpine affinities, other members of the Columbia Bridge assemblage represent species that exemplify the well-known western-eastern North American disjunct pattern. These are: *Salix vestita* (FIGURE 69), *Parnassia* cf. *Kotzebuei*, *Dryas Drummondii* (FIGURE 70), and *Elaeagnus commutata* (FIGURE 71). The place nearest Columbia Bridge where these plants are now found is the Gaspé Peninsula, the present flora of which (Scoggan, 1950) contains all species we identified from the Columbia Bridge beds except *Polygonum ramosissimum*. On floristic grounds, therefore, it seems possible that the present Gaspé flora could in part have been derived from plant populations that no longer exist in northern New England and that might trace back in time and space to even more southern populations.

The region bordering the Gulf of St. Lawrence has long been known to harbor many examples of plants narrowly or broadly disjunct from occurrences in parts of western North America, most notably the northern Rocky Mountain area. Fernald (1925), whose field work in Gaspé and Newfoundland led to the early documentation of this pattern, suggested that the eastern populations persisted through glacial periods in refugia that were untouched by glaciation. These refugia were located essentially where the plants now occur in the East. Fernald's hypothesis, which was consistent with the geological and botanical evidence of the day, stimulated much discussion and research, and this has been summarized most recently by Drury (1969; see also Morisset, 1971), with emphasis on the Gulf of St. Lawrence region. Ives (1974) has also reviewed the extensive literature relating to the various ice-free refugia proposed for northern North America and Europe.

Discovery of intermediate stations during the past fifty years makes the eastern North American populations appear much less isolated than they initially seemed to be. For example, Drury (1969) reduced to 45 a list of 532 disjunct species and varieties published by Fernald in support of his hypothesis of unglaciated refugia. Also, there is agreement on geological evidence of glaciation in proposed nunatak areas near the Gulf of St. Lawrence, although the age of the glacial scouring and erratics remains unknown (Drury, 1969). Rousseau (1953), whose work in northern Quebec resulted in the discovery there of many of the "western" North



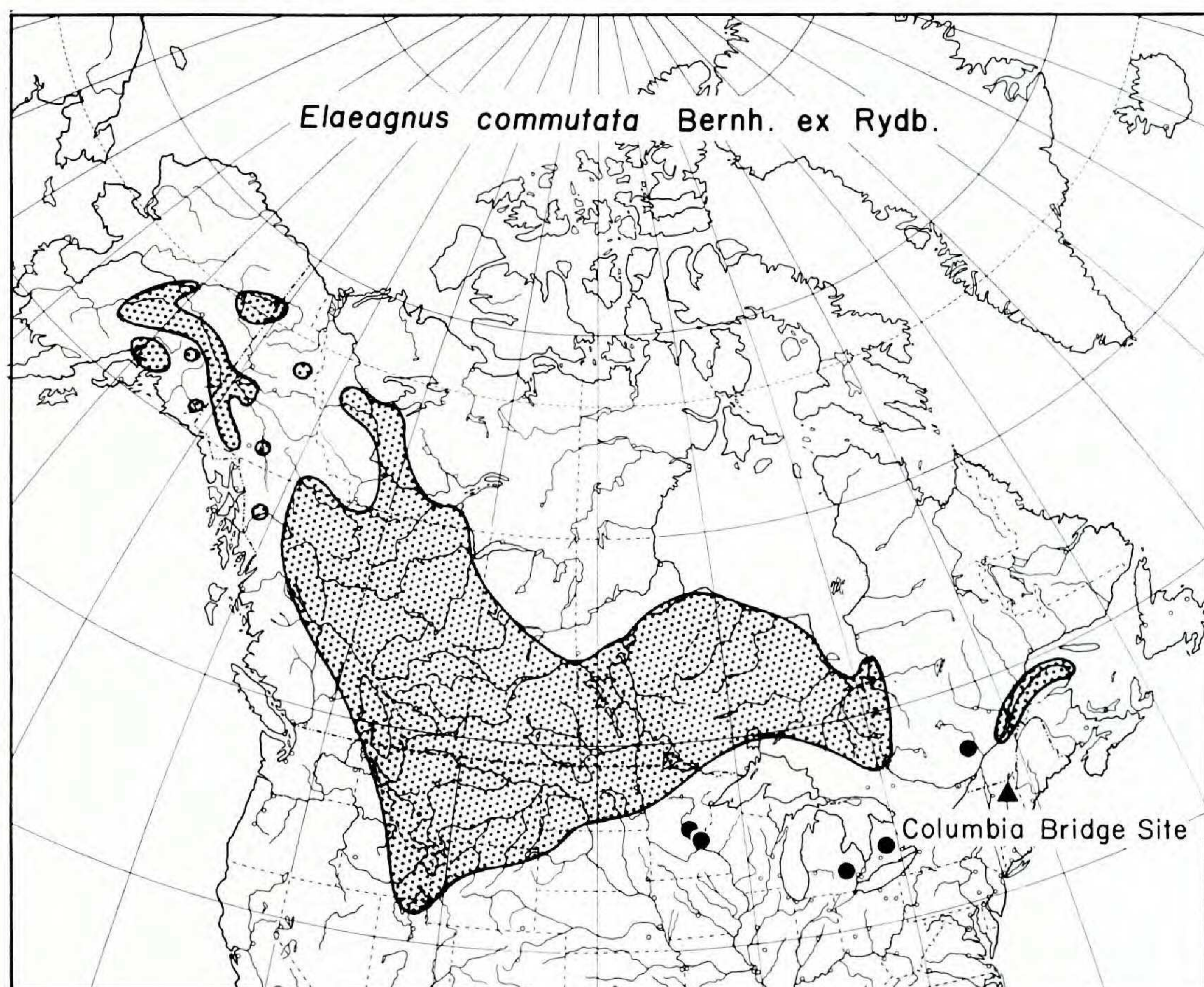
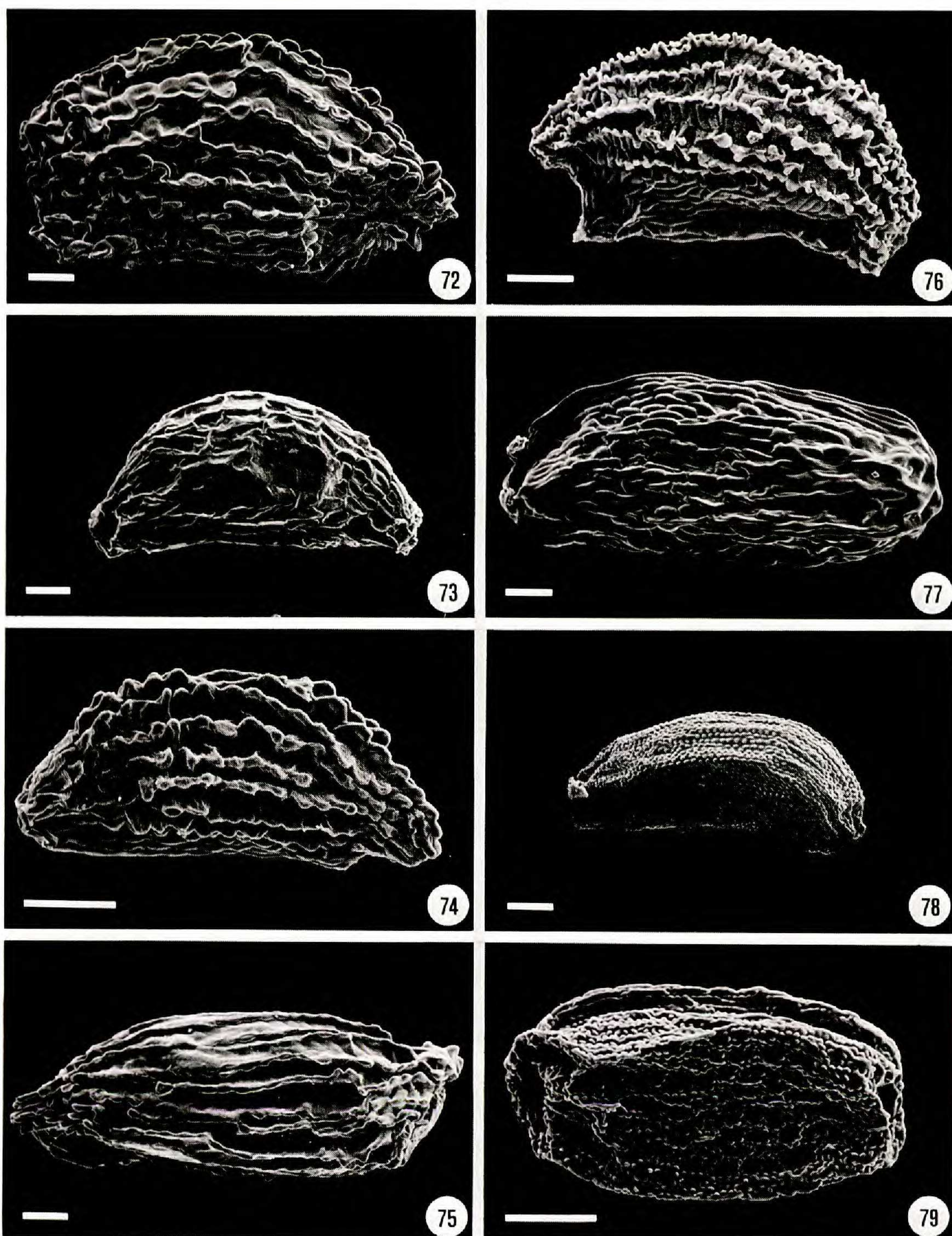


FIGURE 71. North American distribution of *Elaeagnus commutata* based on maps in Hultén (1968) and C. Rousseau (1974). Dots show locations of late Wisconsinan pollen records (Andersen, 1954; Birks, 1976; Cushing, 1967; Sigleo & Karrow, 1977; dot in Quebec refers to three sites in Mauricie National Park where *E. commutata* pollen occurs in late and postglacial sediments, data courtesy of P. Richard, University of Montreal). Triangle shows location of Columbia Bridge site.

American species listed by Fernald, has proposed an alternative to the nunatak hypothesis, namely that as Quaternary glaciers receded, an "arctic corridor" adjacent to the ice sheet provided suitable conditions for eastward migration of species. Rousseau related the present occurrence of "western" plants on the Gaspé to postglacial colonization and persistence in suitable habitats. Thus, in Rousseau's view, the plants were late glacial relicts, whereas Fernald considered them relicts of preglacial times.

Few paleobotanical data have been cited in support of either hypothesis. However, the Columbia Bridge fossils show that at least some western-eastern North American disjuncts were present in eastern North America on recently deglaciated terrain during late glacial time. One of these, *Elaeagnus commutata*, which is distributed almost continuously from western to eastern North America, has other late glacial occurrences (FIGURE 71) beyond its present range, suggesting that the gap may be of recent origin. The Columbia Bridge fossils generally support Rousseau's hypothe-





FIGURES 72–79. Scanning electron micrographs, seeds of northeastern North American species of *Saxifraga*. 72–76, Sect. MICRANTHES (Haw.) D. Don: 72, *S. hieracifolia* (U.S.A., Alaska, Alaska Highway mile 1234, *Raup & Raup* 12869, 16 Aug. 1944 (A)); 73, *S. nivalis* (Canada, Québec, e. coast Hudson Bay, Flaherty Island, *Abbe & Abbe* 4093, 30 Aug. 1939 (GH)); 74, *S. virginiensis* (U.S.A., New Hampshire, Coös Co., summit of Crag, *Deane s.n.*, 28 May 1919 (GH)); 75, *S. pennsylvanica* (U.S.A., Massachusetts, Plymouth Co., Plymouth, *Boott s.n.*, 23 Sept. 1853 (GH)); 76, *S. stellaris* (Greenland, Sukkertoppen District, 65°25' N., 52°41' W., *Porsild* 8063, 4 Aug. 1940 (GH)). 77, 78, Sect. HIRCULUS Tausch: 77, *S. Hirculus* (U.S.A., Alaska, Kotzebue Sound, *Scamman*



sis of late glacial migration and establish that some of the "western" species cited by Fernald as indicating iceless refugia were in fact present on glaciated surfaces south of their areas of present occurrence.

It seems possible that edaphic and climatic conditions during late glacial time may have been appropriate for rapid plant migration, not only from west to east but in the opposite direction and, of course, from south to north. The fossil record must be more complete before the details of these migrations can be worked out. Within glaciated North America the western-eastern pattern of plant disjunction may be a result of postglacial range disruption in species that achieved transcontinental distributions during late glacial time. Eastern or western populations may also have had a history in either or both regions that predates the period of final ice withdrawal, as is the case with *Elaeagnus*, whose pollen (Sigleo & Karrow, 1977) occurs in a late Wisconsin interstadial deposit in Ontario (FIGURE 71). For glaciated regions the best approach to the problem of how ranges of plants developed is clearly to acquire a detailed record based on fossils.

#### SUMMARY

Rhythmically laminated sediments from the upper Connecticut River valley near Columbia Bridge have been radiocarbon dated at  $11,390 \pm 115$  and  $11,540 \pm 110$  years B.P. The deposit has been interpreted as glaciolacustrine, suggesting that a local glacier was present in northern New England at the time the sediments accumulated. The continental ice-sheet margin was in the St. Lawrence River valley 11,500 years ago.

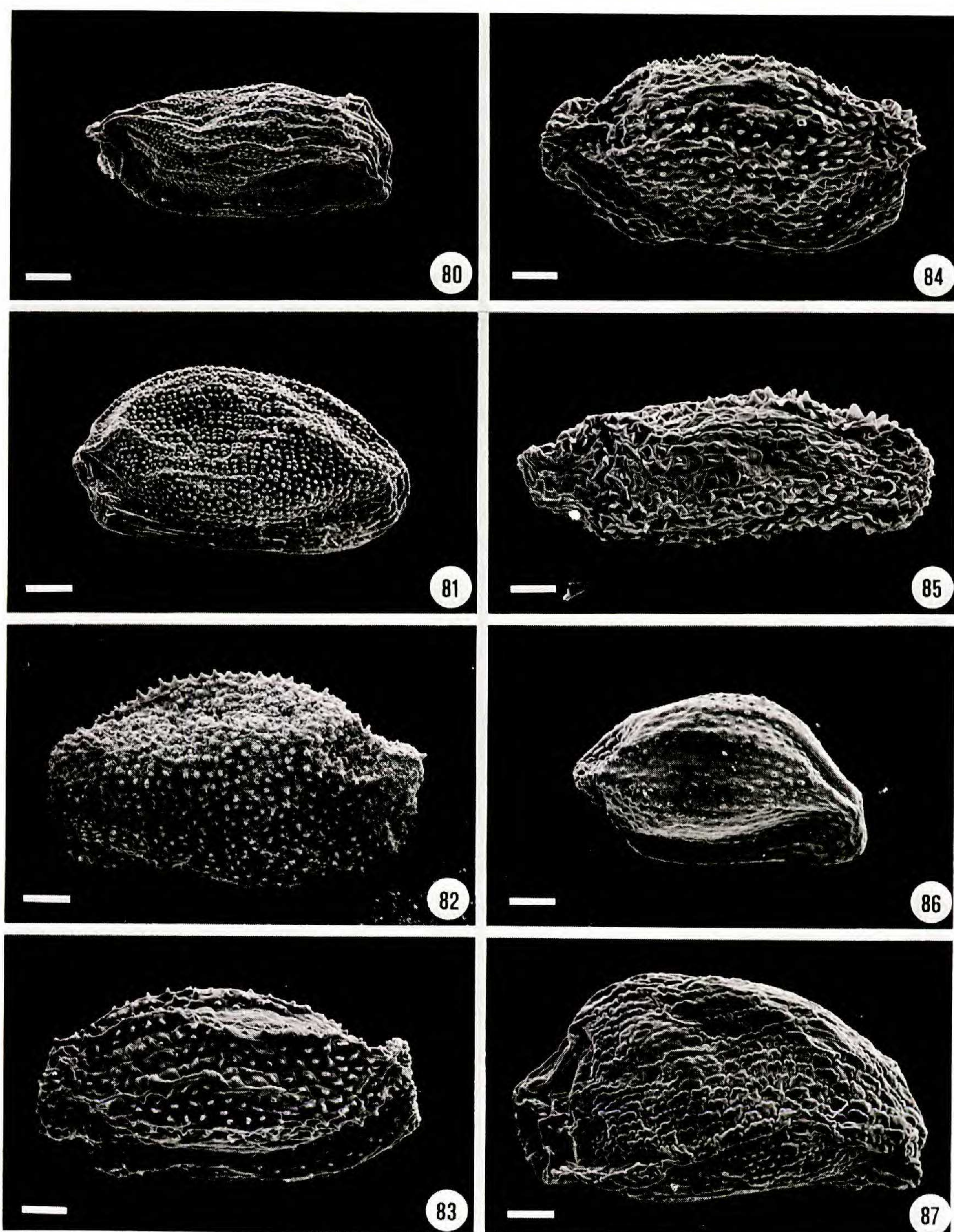
Pollen and plant macrofossils from the sediments indicate that, although the landscape near the fossil site was predominantly treeless, a diverse flora of mosses, herbs, woody plants of herblike habit, and shrubs was established. Spruce and balsam poplar are minor components of the fossil assemblage. The mosses are nearly all species of wet to dry calcareous habitats, but both calcicolous and noncalcicolous seed plants are represented. This suggests that the absence of competition from trees and soil immaturity may have allowed heterogeneous associations of species to exist. Many of the seed plants are pioneers, and some play an important role in the revegetation of deglaciated terrain in areas of current alpine glaciation. The fossil assemblage includes *Dryas* (2 species), *Elaeagnus*, and *Shepherdia*, which, by virtue of nitrogen-fixing symbionts, presumably helped to enrich the raw glacial soils.

On the basis of identified macrofossils, the Columbia Bridge flora was broadly northern in composition. It consisted of arctic-alpine species (all of which are presently very rare in New England), boreal and subarctic

---

6466, 17-27 Aug. 1951 (GH)); 78, *S. flagellaris* (Canada, N.W.T., e. slope Richardson Mts.,  $68^\circ$  N.,  $136^\circ$  W., Porsild 6828, 15-17 Aug. 1933 (GH)). 79, Sect. SAXIFRAGA: *S. rivularis* (Canada, N.W.T., e. slope Richardson Mts., west Mackenzie River delta, Porsild 6826, 15-17 Aug. 1933 (GH)). White bars = 100  $\mu$ m.





FIGURES 80–87. Seeds of northeastern North American species of *Saxifraga*. 80, Sect. SAXIFRAGA: *S. cespitosa* (Canada, Québec, Richmond Gulf, e. coast Hudson Bay, *Abbe et al.* 3601, 1 Aug. 1939 (GH)). 81, Sect. TRACHYPHYLLUM Gaudin: *S. tricuspida* (Canada, Québec, Port Harrison, e. coast Hudson Bay, *Malte* 12089, 18–20 Aug. 1928 (GH)). 82–85, Sect. XANTHIZOON Griseb., *S. aizoides*: 82, fossil seed from Columbia Bridge site, cell walls obscured by mineral particles; 83, 84, two seeds from same capsule, herbarium specimen (Canada, Newfoundland, Bonne Bay region, *Fernald & Wiegand* 3521, 27 Aug. 1910 (GH)); 85, less mature seed from herbarium specimen showing broader, less contracted papillae than those in Figures 83, 84 (Canada, Québec, Bonaventure



plants, and a few species that now show an eastern-western North American pattern of disjunction. The disjunct eastern populations were at one time thought to indicate the existence of unglaciated refugia in the area adjacent to the Gulf of St. Lawrence, but the fossils show that some species with this pattern grew on recently deglaciated surfaces south of their present area of occurrence. The distribution of such plants may have been much wider in late glacial time than is now the case, although the suggestion that western plants may have migrated eastward during the time of general ice recession must await confirmation from more paleobotanical evidence. Some of them may have had a long history of occurrence in the East.

#### ACKNOWLEDGMENTS

We are very grateful for help received from the following specialists who commented on named or unnamed fossil material submitted for their review: George W. Argus (*Salix*), Robert R. Haynes (*Potamogeton*), and Richard S. Mitchell (*Polygonum*). Our colleagues at the Arnold Arboretum and the Gray Herbarium were helpful sounding boards and sources of information during the time the macrofossils were being identified. Two of the radiocarbon dates were obtained through the kind efforts of Margaret Bender and Thompson Webb, III. The pipette analyses were done by F. T. Retelle. Robin S. Lefberg expertly drew Figures 14–28, 30, and 31. Use of Nitex screening in sample processing was suggested by Christine Manville. The scanning electron microscopy was done by Edward A. Seling in a laboratory supported by NSF Set-up Grant BMS-7412494. We also acknowledge with thanks the comments of J. H. Hartshorn, D. A. Livingstone, P. Richard, and C. E. Wood, Jr., who read an early draft of the manuscript. Work on the Columbia Bridge site was aided by a grant from the Milton Fund of Harvard University.

#### LITERATURE CITED

- AALTO, M. 1970. *Potamogetonaceae* fruits. I. Recent and subfossil endocarps of the Fennoscandian species. 85 pp. *Acta Bot. Fenn.* 88.
- ANDERSEN, S. T. 1954. A late-glacial pollen diagram from southern Michigan, U. S. A. *Danmarks Geol. Undersøg.* II. 80: 140–155. *pls. VIII, XIII.*
- ARGUS, G. W., & M. B. DAVIS. 1962. Macrofossils from a late-glacial deposit at Cambridge, Massachusetts. *Am. Midl. Nat.* 67: 106–117.
- ASHLEY, G. M. 1972. Rhythmic sedimentation in glacial Lake Hitchcock, Massachusetts–Connecticut. 148 pp. *Contr. Dept. Geol. Univ. Massachusetts Amherst* 10.

---

Co., Bonaventure River, *Collins et al.* 5222, 5, 6, & 8 Aug. 1904 (GH)). 86, Sect. AIZOONIA Tausch: *S. Aizoon* (Canada, Québec, Gaspé, Grande Vallée, *Rousseau* 31192, 23 July 1928 (GH)). 87, Sect. PORPHYRION Tausch: *S. oppositifolia* (Canada, Québec, Île St.-Charles, Mingan Islands, *Marie-Victorin & Rolland-Germain* 18802, 26 July 1924 (GH)). White bars = 100  $\mu$ m.



- BIRKS, H. J. B. 1976. Late-Wisconsin vegetational history at Wolf Creek, central Minnesota. *Ecol. Monogr.* **46**: 395–429. *3 unpagged fold-out figs.*
- BOIVIN, B. 1966–67. Énumération des plantes du Canada. *Nat. Canad.* **93**: 253–273, 371–437, 583–646, 989–1063; **94**: 131–157, 471–528, 625–656. [Also issued with the same pagination plus an index, pp. I-1 to I-53, in *Provancheria* **6**, n.d.]
- CALDWELL, D. W., C. KOTEFF, & L. S. HANSON. 1978. Age of deglaciation in the lower Merrimac Valley, southern New Hampshire. *Geol. Soc. Am. Abstr. Programs* **10**(2): 35.
- CANNON, W. F. 1964. Pleistocene geology of the Vermont portion of the Averill and Guildhall quadrangles: a report to the State Geologist. Open File Rept. Vermont Geol. Survey, Montpelier. [Unpublished.]
- CONOLLY, A. 1976. Use of the scanning electron microscope for the identification of seeds, with special reference to *Saxifraga* and *Papaver*. *Folia Quat.* **47**: 29–38.
- CRONIN, T. M. 1977. Late-glacial marine environments of the Champlain Valley (New York, Quebec). *Quat. Res.* **7**: 238–253.
- CUSHING, E. J. 1964. Redeposited pollen in late-Wisconsin pollen spectra from east-central Minnesota. *Am. Jour. Sci.* **262**: 1075–1088. *1 fold-out fig.*
- . 1967. Late-Wisconsin pollen stratigraphy and the glacial sequence in Minnesota. Pp. 59–88 + *1 unpagged fold-out fig.* In: E. J. CUSHING & H. E. WRIGHT, JR., eds., *Quaternary paleoecology*. viii + 433 pp. Yale Univ. Press, New Haven.
- DAVIS, M. B. 1958. Three pollen diagrams from central Massachusetts. *Am. Jour. Sci.* **256**: 540–570. *3 fold-out figs.*
- . 1961. The problem of rebedded pollen in late-glacial sediments at Taunton, Massachusetts. *Ibid.* **259**: 211–222.
- . 1965. Phytogeography and palynology of northeastern United States. Pp. 377–401 in: H. E. WRIGHT, JR., & D. G. FREY, eds., *The Quaternary of the United States*. x + 922 pp. Princeton Univ. Press, Princeton, N. J.
- , L. B. BRUBAKER, & T. WEBB, III. 1973. Calibration of absolute pollen influx. Pp. 9–25 in: H. J. B. BIRKS & R. G. WEST, eds., *Quaternary plant ecology*. ix + 326 pp. John Wiley & Sons, New York.
- & J. C. GOODLETT. 1960. Comparison of the present vegetation with pollen-spectra in surface samples from Brownington Pond, Vermont. *Ecology* **41**: 346–357.
- DAVIS, R. B., T. E. BRADSTREET, R. STUCKENRATH, JR., & H. W. BORNS, JR. 1975. Vegetation and associated environments during the past 14,000 years near Moulton Pond, Maine. *Quat. Res.* **5**: 435–465.
- & T. WEBB, III. 1975. The contemporary distribution of pollen in eastern North America: a comparison with the vegetation. *Quat. Res.* **5**: 395–434.
- DONNER, J. J., H. JUNGNER, & Y. VASARI. 1971. The hard-water effect on radio-carbon measurements of samples from Säynäjälampi, north-east Finland. *Comment. Phys.-Math.* **41**: 307–310.
- DRURY, W. H., JR. 1969. Plant persistence in the Gulf of St. Lawrence. Pp. 105–148 in: K. N. H. GREENIDGE, ed., *Essays in plant geography and ecology*. 184 pp. Nova Scotia Museum, Halifax.
- EMERSON, B. K. 1898. Geology of old Hampshire County, Massachusetts, comprising Franklin, Hampshire, and Hampden counties. 790 pp. *maps*. U. S. Geol. Survey Monogr. **29**.



- FENNEMAN, N. M. 1938. Physiography of eastern United States. xiii + 714 pp. *pls. I-VI*. McGraw-Hill Book Company, New York.
- FERNALD, M. L. 1907. The soil preferences of certain alpine and subalpine plants. *Rhodora* 9: 149-193.
- . 1925. Persistence of plants in unglaciated areas of boreal America. *Mem. Am. Acad.* 15: 237-342.
- . 1950. Gray's manual of botany. ed. 8. lxiv + 1632 pp. American Book Company, New York.
- FLINT, R. F. 1951. Highland centers of former glacial outflow in northeastern North America. *Bull. Geol. Soc. Am.* 62: 21-38. 1 *pl.*
- . 1953. Probable Wisconsin substages and late-Wisconsin events in northeastern United States and southeastern Canada. *Ibid.* 64: 897-919. 3 *fold-out pls.*
- . 1956. New radiocarbon dates and late-Pleistocene stratigraphy. *Am. Jour. Sci.* 254: 265-287.
- . 1971. Glacial and Quaternary geology. 892 pp. John Wiley & Sons, Inc., New York.
- GADD, N. R., B. C. McDONALD, & W. W. SHILTS. 1972. Deglaciation of southern Quebec. 19 pp. *Geol. Survey Canada Paper* 71-47.
- GODWIN, H. 1975. The history of the British flora. ed. 2. x + 541 pp. *pls. I-XXVII*. Cambridge Univ. Press, Cambridge, England.
- HANSON, L. S., & D. W. CALDWELL. 1977. Late Wisconsin moraines in northwestern Maine which postdate the marine transgression into the St. Lawrence Valley. *Geol. Soc. Am. Abstr. Programs* 9(3): 272.
- HERMANN, F. J. 1970. Manual of the *Carices* of the Rocky Mountains and Colorado Basin. 397 pp. U. S. Dept. Agr. Agr. Handb. 374.
- HITCHCOCK, C. L., & A. CRONQUIST. 1964. Vascular plants of the Pacific Northwest. Pt. 2. Salicaceae to Saxifragaceae. 597 pp. Univ. Washington Press, Seattle.
- HOLLICK, A. 1931. Plant remains from a Pleistocene lake deposit in the upper Connecticut River valley. *Brittonia* 1: 35-55. *pls. 1-11*.
- HULTÉN, E. 1968. Flora of Alaska and neighboring territories. xxiv + 1008 pp. 8 *pls.* Stanford Univ. Press, Stanford, Calif.
- IVERSEN, J. 1936. Sekundäres Pollen als Fehlerquelle. *Danmarks Geol. Undersøg.* 4(15): 3-24.
- IVES, J. D. 1974. Biological refugia and the nunatak hypothesis. Pp. 605-636 *in*: J. D. Ives & R. G. BARRY, eds., Arctic and alpine environments. xviii + 999 pp. Methuen, London.
- JACOBS, E. C. 1950. Physical features of Vermont. 169 pp. Vermont State Development Commission, Montpelier.
- JESSEN, K. 1955. Key to subfossil *Potamogeton*. *Bot. Tidsskr.* 52: 1-7.
- KAPLAN, K. 1976. Zur Embryologie und Systematik der Gattung *Saxifraga*. *Bot. Jahrb.* 97: 61-71.
- LAMARCHE, R. 1971. Northward moving ice in the Thetford Mines area of southeastern Quebec. *Am. Jour. Sci.* 271: 383-388.
- LARSEN, F. D. 1975. Movement of late Wisconsinan ice in central Vermont as shown by the Barre Granite indicator fan. *Geol. Soc. Am. Abstr. Programs* 7(1): 87, 88.
- . 1978. Retreat of an active ice lobe in the Connecticut Valley, Massachusetts. *Ibid.* 10(2): 72.



- LAWRENCE, D. B., R. E. SCHOENIKE, A. QUISPEL, & G. BOND. 1967. The role of *Dryas drummondii* in vegetation development following ice recession at Glacier Bay, Alaska, with specific reference to its nitrogen fixation by root nodules. *Jour. Ecol.* **55**: 793–813. *pls.* 16, 17.
- LOUGEE, R. J. 1939. Geology of the Connecticut watershed. New Hampshire Fish Game Dept. Biol. Survey Connecticut Watershed. Survey Rep. **4**: 131–149.
- MARTIN, A. C. 1951. Identifying pondweed seeds eaten by ducks. *Jour. Wildlife Managem.* **15**: 253–258.
- MCANDREWS, J. H., & D. M. POWER. 1973. Palynology of the Great Lakes: the surface sediments of Lake Ontario. *Canad. Jour. Earth Sci.* **10**: 777–792.
- MCDOWELL, L. L., R. M. DOLE, JR., M. HOWARD, JR., & R. A. FARRINGTON. 1971. Palynology and radiocarbon chronology of Bugbee Wildflower Sanctuary and Natural Area, Caledonia County, Vermont. *Pollen Spores* **13**: 73–91.
- MILLER, N. G. Studies on North American Quaternary bryophyte subfossils. II. An assemblage from the late glacial of Vermont. [Unpublished manuscript.]
- & W. S. BENNINGHOFF. 1969. Plant fossils from a Cary-Port Huron Interstade deposit and their paleoecological interpretation. *Geol. Soc. Am. Spec. Paper* **123**: 225–248 + 1 fold-out fig.
- MITCHELL, R. S., & J. K. DEAN. 1978. Polygonaceae (buckwheat family) of New York State. 81 pp. New York State Mus. Bull. **431**.
- MORISSET, P. 1971. Endemism in the vascular plants of the Gulf of St. Lawrence region. *Nat. Canad.* **98**: 167–177.
- MOTT, R. J. 1977. Late-Pleistocene and Holocene palynology in southeastern Québec. *Géogr. Phys. Quat.* **31**: 139–149.
- . 1978. *Populus* in late-Pleistocene pollen spectra. *Canad. Jour. Bot.* **56**: 1021–1031.
- MYERS, P. B., JR. 1964. Geology of the Vermont portion of the Averill Quadrangle, Vermont. 69 pp. Vermont Geol. Survey Bull. **27**.
- OCCHIETTI, S., & C. HILLAIRES-MARCEL. 1977. Chronologie <sup>14</sup>C des événements paléogéographiques du Québec depuis 14000 ans. *Géogr. Phys. Quat.* **31**: 123–133.
- PEASE, A. S. 1964. A flora of northern New Hampshire. v + 278 pp. New England Bot. Club, Cambridge, Massachusetts.
- PECK, R. M. 1973. Pollenbudget studies in a small Yorkshire catchment. Pp. 43–60 *in*: H. J. B. BIRKS & R. G. WEST, eds., Quaternary plant ecology. ix + 326 pp. John Wiley & Sons, New York.
- PIGOTT, C. D., & S. M. WALTERS. 1954. On the interpretation of the discontinuous distributions shown by certain British species of open habitats. *Jour. Ecol.* **42**: 95–116.
- POLUNIN, N. 1940. Botany of the Canadian eastern Arctic. Part I. Pteridophyta and Spermatophyta. vi + 408 pp. 1 map. Natl. Mus. Canada Bull. **92**.
- PORSILD, A. E. 1947. The genus *Dryas* in North America. *Canad. Field-Nat.* **61**: 175–192.
- . 1964. Illustrated flora of the Canadian Arctic Archipelago. ed. 2. 218 pp. Natl. Mus. Canada Bull. **146**.
- PREST, V. K. 1969. Retreat of Wisconsin and Recent ice in North America. *Geol. Survey Canada Map* **1257A**.



- RAUP, H. M. 1943. The willows of the Hudson Bay region and the Labrador Peninsula. *Sargentia* 4: 81-127. *pls. I-IV*.
- . 1959. The willows of boreal western America. *Contr. Gray Herb. Harvard Univ.* 185: 3-95.
- RICHARD, P. 1974. Présence de *Shepherdia canadensis* (L.) Nutt. dans la région du parc des Laurentides, Québec, au tardiglaciaire. *Nat. Canad.* 101: 763-768.
- . 1977. Végétation tardiglaciaire au Québec méridional et implications paléoclimatiques. *Géogr. Phys. Quat.* 31: 161-176.
- RITCHIE, J. C., & S. LICHTI-FEDEROVICH. 1967. Pollen dispersal phenomena in arctic-subarctic Canada. *Rev. Palaeobot. Palynol.* 3: 255-266.
- ROULEAU, E. 1956. The genus *Dryas* (Rosaceae) in Newfoundland. *Contr. Inst. Bot. Univ. Montréal* 69: 5-19. *pls. 1-5*.
- ROUSSEAU, C. 1974. Géographie floristique du Québec-Labrador. xiv + 799 pp. Travaux et documents du Centre d'Études nordiques 7. Les Presses de l'Université Laval, Québec.
- ROUSSEAU, J. 1953. The value of botany as indicator of unglaciated areas. *Proc. VII Pacific Sci. Congr.* 5: 178-186.
- SANGSTER, A. G., & H. M. DALE. 1964. Pollen grain preservation of underrepresented species in fossil spectra. *Canad. Jour. Bot.* 42: 437-449.
- SCHAFER, J. P. 1968. Retreat of the last ice sheet from New England. [Abstr.] *Geol. Soc. Am. Spec. Paper* 115: 291.
- & J. H. HARTSHORN. 1965. The Quaternary of New England. Pp. 113-128 in: H. E. WRIGHT, JR., & D. G. FREY, eds., *The Quaternary of the United States*. x + 922 pp. Princeton Univ. Press, Princeton, N. J.
- SCOGGAN, H. J. 1950. The flora of Bic and the Gaspé Peninsula, Quebec. 399 pp. *pl. I*. *Natl. Mus. Canada Bull.* 115.
- SEYMOUR, F. C. 1969. The flora of New England. xvi + 596 pp. Charles E. Tuttle Company, Rutland, Vermont, and Tokyo.
- SHILTS, W. W. 1976. Glacial events in southern Quebec-northern New England, a reappraisal. *Geol. Soc. Am. Abstr. Programs* 8(2): 267.
- SIGLEO, W. R., & P. F. KARROW. 1977. Pollen-bearing Erie interstadial sediments from St. Marys, Ontario. *Canad. Jour. Earth Sci.* 14: 1888-1896.
- SILVESTER, W. B. 1977. Dinitrogen fixation by plant associations excluding legumes. Pp. 141-190 in: R. W. F. HARDY & A. H. GIBSON, eds., *A treatise on dinitrogen fixation. Sect. IV. Agronomy and ecology*. xii + 527 pp. John Wiley & Sons, New York.
- SPEAR, R. W. 1978. The pollen record of high elevation sites in the White Mountains of New Hampshire. *Abstr. Am. Quat. Assoc. 5th Biennial Meeting*, p. 178.
- STEWART, D. P., & P. MACCLINTOCK. 1969. The surficial geology and Pleistocene history of Vermont. 251 pp. *Vermont Geol. Survey Bull.* 31.
- & ———. 1970. Surficial geologic map of Vermont. *Vermont Geol. Survey*, Montpelier.
- STONE, B. D., & C. KOTEFF. 1973. A late Wisconsinan ice readvance in the Merrimack River valley, southern New Hampshire. *Geol. Soc. Am. Abstr. Programs* 5(2): 223.
- STUIVER, M. 1978. Carbon-14 dating: a comparison of beta and ion counting. *Science* 202: 881-883.
- TRAVERSE, A. 1955. Pollen analysis of the Brandon Lignite of Vermont. iv + 107 pp. U. S. Dept. Int. Bur. Mines Rept. Invest. 5151.



- VEROSUB, K. L. 1975. Validation of the varve chronology of early glacial Lake Hitchcock, western New England. *Geol. Soc. Am. Abstr. Programs* 7(7): 1307.
- WAGNER, W. P., J. D. MORSE, & C. C. HOWE. 1972. Till studies, Shelburne, Vermont. Pp. 377–397 *in*: Guidebook for field trips in Vermont. New England Intercol. Geol. Conf. 64th Annual Meet.
- WHITE, W. W. 1956. Native willows found in Montana. *Proc. Montana Acad.* 16: 21–35.
- WHITEHEAD, D. R., & D. R. BENTLEY. 1963. A post-glacial pollen diagram from southwestern Vermont. *Pollen Spores* 5: 115–127.

APPENDIX A. Percentages of pollen and spores from the Columbia Bridge site not included in pollen diagram.

- Tsuga*: 0.3% (1.00–1.05 m.), 0.2% (1.10–1.15 m.), 0.5% (3.49–3.59 m.).
- Larix*: 0.2% (1.55–1.60 m.).
- Populus*: 0.3% (0.40–0.45 m.), 1.1% (0.90–0.95 m.), 0.3% (1.10–1.15 m.), 0.2% (1.20–1.25 m.), 0.2% (1.30–1.35 m.), 0.2% (1.50–1.55 m.), 0.2% (3.49–3.59 m.).
- cf. *Engelhardtia*: 0.5% (0.50–0.55 m.), 0.2% (0.60–0.65 m.), 0.7% (0.70–0.75 m.), 0.6% (0.80–0.85 m.), 1.8% (1.10–1.15 m.), 1.1% (1.55–1.60 m.).
- cf. *Platycarya*: 1.2% (0.80–0.85 m.), 0.2% (1.35–1.40 m.).
- Juglans*: 0.7% (0.40–0.45 m.), 0.3% (0.60–0.65 m.), 0.2% (1.20–1.25 m.).
- Fagus*: 0.3% (0.30–0.35 m.), 0.2% (1.20–1.25 m.), 0.2% (1.55–1.60 m.).
- Castanea*: 0.5% (3.49–3.59 m.).
- Ulmus*: 0.5% (0.20–0.25 m.), 0.3% (0.40–0.45 m.), 0.6% (0.80–0.85 m.), 0.3% (0.90–0.95 m.), 0.2% (1.10–1.15 m.), 0.4% (1.20–1.25 m.), 0.4% (1.50–1.55 m.), 0.2% (1.55–1.60 m.), 0.5% (3.49–3.59 m.).
- Ericaceae: 0.2% (0.20–0.25 m.), 0.3% (0.30–0.35 m.), 0.4% (0.40–0.45 m.), 0.3% (0.90–0.95 m.), 0.3% (1.00–1.05 m.), 0.6% (1.20–1.25 m.), 0.2% (1.30–1.35 m.), 0.2% (1.50–1.55 m.).
- cf. *Dryas Drummondii*: 0.3% (0.10–0.15 m.), 0.2% (0.30–0.35 m.).
- Other Rosaceae: 0.2% (3.49–3.59 m.).
- Chenopodiaceae-Amaranthaceae: 0.5% (0.30–0.35 m.), 0.3% (0.60–0.65 m.), 0.6% (0.80–0.85 m.), 0.2% (1.30–1.35 m.), 0.2% (1.50–1.55 m.).
- Nymphaea*: 0.3% (3.49–3.59 m.).
- Typha latifolia*: 0.4% (0.30–0.35 m.), 0.2% (1.55–1.60 m.).
- Sparganium*: 0.2% (0.30–0.35 m.), 0.3% (0.40–0.45 m.).
- Botrychium*: 0.2% (0.40–0.45 m.), 0.1% (1.10–1.15 m.), 0.3% (1.50–1.55 m.), 0.3% (1.55–1.60 m.), 0.2% (3.49–3.59 m.).

APPENDIX B. Morphological notes on seeds and fruits.

**Arenaria.** Seeds of the 20 native sandworts listed by Fernald (1950; only northern species examined) and Boivin (1966–67) differ in size (largest, *A. peploides* L., to 4 mm. long; smallest, *A. rubella* (Wahlenb.) Sm., ca. 0.5 mm. long); in shape (from side, more or less elliptic in most, angular in *A. groenlandica* (Retz.) Sprengel); in having (*A. capillaris* Poiret s. l., *A. laricifolia* L., *A. marcescens* Fern.) or lacking a beak near the hilum; in having (*A. lateriflora* L., *A. macrophylla* Hooker) or lacking a strophiole; in the presence (*A. macro-*



*carpa* Pursh) of a crest of enlarged finger-like cells; and in cellular configuration of the seed coat (black and shiny, adjoining cell walls just visible with the dissecting microscope (*A. lateriflora* L., *A. lanuginosa* (Michaux) Rohrb.) or not discernible (*A. macrophylla* Hooker), adjoining cell walls strongly undulate (*A. caroliniana* Walter), moderately undulate (*A. capillaris* Poiret; *A. dawsoneensis* Britton, FIGURE 32; *A. humifusa* Wahlenb.; *A. patula* Michaux, FIGURE 36; *A. Rossii* R. Br., FIGURE 35; *A. rubella*; *A. stricta* Michaux, FIGURE 37), weakly undulate (*A. groenlandica* (Retz.) Sprengel), or adjoining walls mostly not discernible but seed coat brown rather than black and shiny (*A. sajanensis* Willd.)). Seed-coat cells can be seen under a dissecting microscope at high magnification, but scanning electron microscopy is necessary for appraisal of detail.

**Saxifraga.** Of the sixteen species of *Saxifraga* attributed to northeastern North America by Fernald (1950), Polunin (1940), and Scoggan (1950), we have evaluated external seed morphology by scanning electron microscopy in all but *S. cernua* L., *S. gaspensis* Fern., and *S. Geum* L., for which seeds were not available. Seeds of the species studied are ellipsoid or oblong, and when dry (usually also when wet) have one, or sometimes two, prominent longitudinal folds. Variation is also discernible in size (smallest, ca. 0.5 mm., *S. virginensis* Michaux, FIGURE 74; *S. rivularis* L., FIGURE 79), shape, and length to width ratios. Configuration of the mature seed coat seems to differ consistently from species to species. Seed coat differences can reflect maturity (cf. seeds from ripe capsule, FIGURES 83, 84, vs. immature seed, FIGURE 85); thus, the most meaningful comparisons are made between fully mature seeds. Outer walls of seed coat cells can be strongly bulging (*S. hieracifolia* Waldst. & Kit., FIGURE 72; *S. stellaris* L., FIGURE 76; *S. virginensis* Michaux, FIGURE 74; *S. pensylvanica* L., FIGURE 75), weakly bulging (*S. nivalis* L., FIGURE 73; *S. Hirculus* L., FIGURE 77), or elaborated into long and spinelike (*S. aizoides* L., FIGURES 83, 84) or short, sharply defined (*S. Aizoon* L., FIGURE 86) papillae. Papillae or bulging cells are often arranged in longitudinal rows that can be seen with a dissecting microscope. Outer walls of seed coat cells can also be pluripapillose (*S. cespitosa* L., FIGURE 80; *S. flagellaris* Willd. ex Sternb., FIGURE 78; *S. oppositifolia* L., FIGURE 87; *S. rivularis* L., FIGURE 79; *S. tricuspidata* Rottb., FIGURE 81), although anticlinal cell walls may not be fully apparent. Kaplan (1976) has drawn attention to morphological differences in seed coats of certain European alpine species of *Saxifraga*, as has Conolly (1976).

**Potentilla.** Achenes of *Potentilla*, *Fragaria*, and *Sibbaldia* are of similar size and general appearance. However, in each genus the achene apex differs in the following ways (Godwin, 1975): central and obtuse (*Sibbaldia*, FIGURE 28); blunt and ventrally inclined (*Potentilla*, FIGURE 29); pointed and strongly inclined (somewhat hooked) toward the ventral suture (*Fragaria*). Achenes of certain species of *Potentilla* are sufficiently distinct to allow identification of well-preserved fossil material, providing accurately determined comparative specimens are at hand. Species (notes pertain to native northern taxa in Fernald (1950) and to all species in Polunin (1940) and Scoggan (1950)) differ in having achenes densely hairy (*P. fruticosa* L., *P. tridentata* Aiton); the achene surface smooth or finely to coarsely ridged (*P. anglica* Laich., *P. canadensis* L., *P. Crantzii* (Crantz) G. Beck, *P. effusa* Douglas, *P. erecta* (L.) Hampe, *P. millegrana* Engelm., *P. nivea* L., *P. norvegica* L., *P. pectinata* Raf., *P. pensylvanica* L., *P. pulchella* R. Br., *P. tridentata* Aiton, and *P. rivalis* Nutt.); the dorsal su-



ture prominent (*P. anserina* L., *P. Egedei* var. *groenlandica* (Tratt.) Polunin); the ventral suture enlarged and ridged (*P. Nicolletii* (S. Watson) Sheldon, *P. paradoxa* Nutt., *P. rivalis* Nutt.); the ventral suture long in relation to total achene length (*P. pensylvanica* L.); and in the size of the achene (e.g., smallest (0.75 mm. high, 0.5 mm. wide), *P. millegrana* Engelm., *P. pentandra* Engelm.). Achenes of *P. arguta* Pursh are similar to those of *Fragaria* in having a short, apical, ventrally oriented, beaklike projection.

N. G. M.

ARNOLD ARBORETUM  
AND GRAY HERBARIUM  
HARVARD UNIVERSITY  
22 DIVINITY AVENUE  
CAMBRIDGE, MASSACHUSETTS 02138

G. G. T.

DEPARTMENT OF EARTH SCIENCES  
SALEM STATE COLLEGE  
SALEM, MASSACHUSETTS 01970